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Fishery Bulletin

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Vol. 76, No. 2 April 1978

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Seattle, Washington

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NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

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ASPECTS OF ESTUARINE INTERTIDAL ECOLOGY OF JUVENILE STRIPED MULLET, *MUGIL CEPHALUS*, IN HAWAII[1]

PETER F. MAJOR[2]

ABSTRACT

Behavior and distribution of schools of young striped mullet, *Mugil cephalus*, were examined in the field and laboratory. Prejuvenile fish approximately 20 mm standard length leave the open ocean to enter intertidal estuarine regions, where they select the shallowest water, areas with extensive diel temperature and salinity fluctuations. At about 50 mm standard length, the mullet move into deeper intertidal waters. It is at this size that mullet are thought to have completed their metamorphosis to juveniles. In a vertical thermal gradient, fish generally <50 mm standard length selected final mean temperatures of 30.0°-32.4°C at the salinities tested (0, 15, 34‰). In the field, they were found in water with high (34.0°-37.2°C), often near lethal (39.0°-42.5°C), temperatures in shallow pools with salinities of 2-30‰. Juveniles generally >50 mm experimentally selected final mean temperatures of 29.0°C at 34‰ salinity to 19.5°C at 0‰ salinity. In the field, fish ≥50 mm remained seaward of the tide line in water of lower and more uniform temperature and higher and more uniform salinity than those recorded for mullet <50 mm. Mullet <50 mm occur seasonally when there are a maximum number of low tides ≤0.0 mm and a minimum number of high tides ≥0.6 m. This allows the mullet increased time to feed undisturbed in areas where there are no predators and intraspecific and possible interspecific competitors for food and space. By the time fish reach 50 mm standard length, the tidal situation changes, allowing predators and competitors access to the shallow areas during low tide. When in the presence of predators, the schooling habit increases chances of survival for individual mullet.

The marine environment includes the highly complex estuarine and intertidal habitats, which undergo continuous fluctuation. Organisms dwelling within these areas must be able to tolerate or escape from the consequences of extreme temperature and salinity oscillations brought about by tidal and meteorological changes. Coral and rocky intertidal tidepools and the estuarine environment serve as nursery and feeding grounds for the young of many species of fishes (Randall 1961; Norris 1963; Lauff 1967; Carr and Giesel 1975).

The purpose of this study was twofold: to determine whether young striped mullet, *Mugil cephalus* Linnaeus, select specific environmental conditions, particularly with respect to temperature and salinity, as found in intertidal estuarine environments in Hawaii, and to explore the possible causal mechanisms that might lead to the selection of such conditions. An experimental vertical thermal gradient (use of such gradients was reviewed by Mantelman 1958; Ivlev and Leizerovich 1960; Fry 1964) in a tank was used to study the relationship between salinity and temperature and the distribution of schools of young striped mullet, and field observations were made of the distribution, feeding, and predator-prey behavior of schooled mullet.

METHODS AND MATERIALS

Field Sites and Capture of Fish

Young striped mullet were observed and collected in estuarine intertidal habitats at a number of locations on the island of Oahu (Figure 1) in the Hawaiian Archipelago during 1972 and 1973. All experimental fish were captured with hand or beach seines near stream mouths or springs and on tidal mud flats in Maunalua Bay on the southeast side of the island. Schools were usually caught in the morning at low tide and transported <16 km to the Oceanic Institute, Makapuu, Oahu.

Observations were made along Wailupe Beach, Wailupe Stream, and Kuapa Pond Streams (Hawaii Kai Development drainage culverts) in Maunalua Bay, and along Kahana River and a silted Hawaiian fishpond in Kahana Bay on the east side

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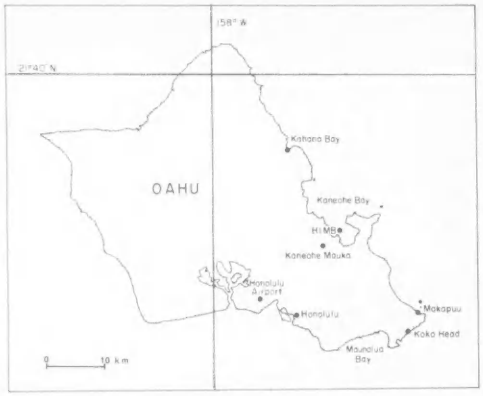


FIGURE 1.—The island of Oahu, Hawaii, showing the major study areas and the locations at which environmental data were collected.

of Oahu. Observations were made primarily during daylight hours, but a few night observations were made as well at Kahana River and Wailupe Beach. Field observations were recorded as I followed at a distance schools of mullet as they swam about estuarine intertidal regions and estuarine streams. Information about the distribution of mullet was also collected by using seines. Behavioral and distributional records were kept and the temperature and salinity of the water through which the fish passed were measured with a telethermometer and compensated salinity refractometer, respectively.

Young *Mugil cephalus* were distinguished and differentiated from the young of a second sympatric species of mullet, *Chelon engeli*, an introduced species (Randall and Kanayama 1972), by differences in body pigmentation pattern and opercle coloration. In addition, young *C. engeli* ≤50 mm standard length (SL) occurred in the intertidal estuarine regions predominantly during the summer and fall, whereas, striped mullet predominated in the winter and spring months. Only observations of mullet that were unquestionably identified as striped mullet were used in this report.

Experimental Methods

Experiments were carried out at the Oceanic Institute during 1972 and 1973 (Table 1). An experimental thermal vertical gradient was established in a 566-l cylindrical Plexiglas[3] tank, 91 cm high and 89 cm in diameter, inside a lighttight enclosure (Figure 2). Epoxy-coated copper coils spiraled around the inside of the tank, having entered through the surface above and through the side at the bottom. These separate sets of coils exited at midtank through the side. Pumps con-

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

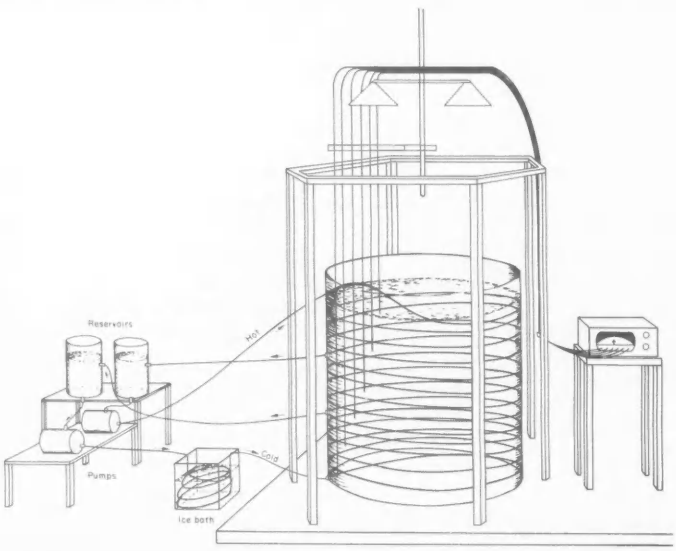


FIGURE 2.—Experimental apparatus (diagramatic). Light excluding sides and covering have been removed from frame.

TABLE 1.—Summary of experimental conditions and fish statistics.

Experimental salinity (‰) (actual test salinity)	Month and year of experiments	Min-max tank temp (°C)	Number fish in size range (mm SL)								Length to nearest mm		Total number fish	Experimental group code (see Figure 3)
			17-19	20-29	30-39	40-49	50-59	60-69	70-79	80-130	Mean	(range)		
34(32)	Feb. 1972	16.8-36.0	2	36							24	(19-28)	38	A1, 2, 3
32	Mar. 1972	15.1-38.6		39	11						27	(21-38)	50	
34	Mar. 1972	17.0-40.1		3	29	2					34	(29-43)	34	
			2	78	40	2					28	(19-43)	122	
34(33)	May 1972	17.8-40.8			7	29	2				42	(37-52)	38	B1, 2, 3
33	May 1972	17.5-41.0				14	17				51	(46-59)	31	
					7	43	19				46	(37-59)	69	
34(36)	July 1972	15.8-39.2					5	4	7	2	68	(55-83)	18	C1, 2, 3
34	July 1972	15.0-39.2					7	3	10	11	75	(56-98)	31	
32	Mar. 1973	15.0-37.8				1		5	9	22	80	(48-103)	37	
32	Mar. 1973	17.0-40.0								20	109	(82-129)	20	
						1	12	12	26	55	82	(48-129)	106	
15(16)	Jan. 1972	16.9-40.0		13	3						27	(24-31)	16	D1, 2, 3
(14)	Mar. 1973	13.0-39.0	1	39							26	(19-29)	40	
(15)	Mar. 1973	13.2-39.9		27	23						28	(20-39)	50	
			1	79	26						26	(19-39)	106	
15(14)	Aug. 1972	15.5-39.8						1	3	18	88	(69-114)	22	E1, 2, 3
15	Mar. 1973	14.1-39.8							1	10	98	(75-125)	11	
								1	4	28	92	(69-125)	33	
0	Feb. 1972	15.9-36.9		26	4						26	(22-34)	30	F1, 2, 3
·	Mar. 1972	16.4-38.9	2	36							22	(19-26)	38	
·	Mar. 1972	16.0-40.1	1	47	10						27	(17-34)	58	
·	Mar. 1973	14.8-39.0		35	2						26	(21-31)	37	
			3	144	16						24	(17-34)	163	
0	May 1972	17.0-38.5			10	19	4				43	(35-51)	33	G1, 2, 3
0	Jan. 1973	18.8-38.2							1	35	98	(76-118)	36	H1, 2, 3
·	Mar. 1973	16.2-38.6								16	102	(87-130)	16	
									1	51	99	(76-130)	52	

nected to reservoirs circulated water, chilled as it passed through a set of coils in an ice bath, before entering the bottom of the tank, and water heated by a braided glass heating tape wrapped around a section of the coil, before it passed into the tank at the surface. The reservoirs allowed air bubbles to escape and the addition of water to the coils.

Vinyl-coated thermistor probes (and leads), extending through plastic tubes to various levels in the tank, ran above the top of the tank and out to a telethermometer recorder.

Fine mesh plastic window screen was attached to the inside circumference of the coils to keep fish in the central area of the tank. The volume of water in the tank available to the fish was approximately 486 l, 88 cm in diameter and 80 cm deep. Observations were made through narrow eye-width slits cut at various levels in each side of the enclosure. A light-excluding cover surrounded the observer during observations. The viewing slits were closed when not in use.

Water samples were taken from the surface, middepth, and bottom before and after each experiment for oxygen, pH, and salinity analysis. Oxygen measurements could not be made continuously during the experiments, but oxygen measurements before and after each experiment did not change noticeably. In addition, respiratory movements of mouth and opercles, which might have been indicative of oxygen deficiencies, in the mullet did not change with increased heating. The above measurements were made primarily to ensure that mullet were not orienting to factors other than temperature.

Illumination was provided by two 15-W incandescent light bulbs fixed in reflectors 84 cm above the surface of the water. Due to the position and low wattage of the light sources, a light gradient was established in the tank. The behavioral and distributional responses of the fish in a continuously changing thermal environment indicated that orientation to temperature and not light gradients occurred. The same observations were used to control for any orientation to pressure gradients, which inevitably existed in the 80-cm deep tank.

One of three experimental salinity conditions, freshwater (range 0-2‰), 15‰ (range 14-16‰), and 34‰ (range 30-36‰), was established prior to placing the fish in the tank. Freshwater was

thoroughly mixed with seawater of 36‰ salinity until a desired salinity was obtained in the tank. Frequently, schools of fish in the field were not caught in water of identical salinity to that used experimentally. Before placing these fish in the experimental tank, freshwater slowly ran into the container of water in which the fish were transported to the laboratory. When the desired lower salinity was reached by dilution and overflow of the water in the container (this required about 60 min to accomplish), the fish were transferred by dip net to the experimental tank. The experimental tank had a water temperature within 1° or 2°C of the water in which the fish were caught and transported or in which dilution occurred.

Within 30-60 min after being placed in the tank, schools and individual mullet swam throughout the tank at relatively uniform speeds. Single and grouped individuals "grazed" along the sides and bottom of the screen in the tank. The behavior of the mullet at this time appeared to be similar to the behavior of undisturbed fish observed in the field.

The water in the tank was cooled and heated simultaneously after the fish demonstrated what appeared to be "normal" schooling and grazing behavior. At half-hour intervals the temperature at various levels was recorded and the behavior and depth and temperature distribution of the mullet were noted. The observations required about 1 or 2 min to complete. Observations continued until the vertical distribution of the mullet did not change with respect to specific water temperatures during two or three consecutive observations. This occurred between 4 and 8 h after commencing the experiments, when the maximum water temperature in the tank was between 36.0° and 40.8°C, and the minimum temperature was between 13.0° and 19.0°C. Upon termination of the observations, the heating and chilling equipment was turned off, water samples were collected, and one of the sides of the enclosure around the tank was slowly removed. The lights were dimmed slowly and turned off by a rheostat. The fish were left in the tank overnight, exposed to natural twilight conditions in the evening and morning, the room having a number of large windows. During the evening and overnight periods the tank temperature gradually became more uniform.

Well before a second series of observations was to be made during the next day, the side of the tank's enclosure was replaced, the lights having been turned on during the twilight period by a rheostat. The tank was also oxygenated for approximately 30 min, followed by at least an additional 30-min period during which the tank was not disturbed. The second day of observations served to check on the experimental procedures and results obtained the first day, and to achieve higher tank temperatures than reached during the first day. Statistical comparisons between first and second day activity were not significant ($P \geq 0.05$), indicating that the fish did not change their depth or temperature distributions.

RESULTS

Experimental

Prior to the onset of heating and chilling, fish generally <50 mm SL (Table 1), with one exception, initially concentrated near the surface or in the upper half (40-80 cm) of the tank. Fish in the 30- to 50-mm SL size ranges in 0‰ salinity were initially concentrated in the lower half (0-40 cm) of the tank. Fish generally ≥50 mm SL initially concentrated near or on the bottom, or in the lower half of the tank. However, fish of all sizes continuously moved throughout the 80-cm deep tank, indicating that the light and pressure gradients and the depth of water were not limiting. When left for hours in the tank at constant temperature conditions at each test salinity, the mullet exhibited the same behavior, distribution patterns, and movements as those observed in mullet before heating and chilling were initiated during the experiments. These observations served as a control for the distributional patterns of mullet observed under test conditions.

Experimental results were grouped and analyzed according to test salinities (0, 15, and 34‰) and mullet size ranges (20-30, 30-50, and ≥50 mm SL) (Table 1). There was overlap and occasional fish outside of specific size ranges in some experiments due to the size composition of the individual mullet caught in schools in the field and subsequently put into the experimental tank. The experimental time period was divided for analysis into five observation intervals, each consisting of three observations (i.e., 1 complete hour of observation with observation being made each half hour). Only data for observation intervals 1, 3, and 5 are presented in Figure 3. Each graph consists of open histograms for the temperature and depth distributions for fish of specified size ranges, test salinity, and observation interval. Observations of

depth distribution were made to within 5-cm intervals; the means given in the graphs being the mean of a given interval (e.g., 47.5 cm for 45-50 cm).

Statistical comparisons for depth or temperature distributions were significant (analysis of variance, $P \leq 0.001$) in all but a few cases. The following comparisons were made, the exceptions to $P \leq 0.001$ values being noted in parentheses: 1) between observation intervals for given fish size ranges and test salinity (no exceptions), 2) between salinities for given fish size ranges and observation interval (depth distribution for fish ≥50 mm SL in observation interval 5 and salinities 15 and 34‰ ($P = 0.27$); depth distribution for fish 20-30 mm SL in observation interval 1 and salinities 0 and 15‰ ($P < 0.003$); temperature distribution for fish ≥50 mm SL in observation interval 1 and salinities 0 and 15‰ ($P < 0.002$)), and 3) between size ranges for a given test salinity and observation interval (depth distribution for a salinity of 34‰ in observation interval 5 and fish size ranges 30-50 and ≥50 mm SL ($P < 0.004$); temperature distribution for salinity 34‰ in observation interval 5 and fish size ranges 20-30 and 30-50 mm SL ($P = 0.46$)).

Changes in depth distribution of fish are readily discernable in the histograms in Figure 3. At each test salinity, with the exception of 30-50 mm SL fish at 0‰ salinity, mullet ≤50 mm SL moved downwards in the tank to a mean depth of 47.5 or 52.5 cm by the last observation interval. Fish ≥50 mm SL moved up to mean depths of 32.5 to 42.5 cm. Fish 30-50 mm SL at 0‰ moved from an initial distribution in the bottom half of the tank to a mean of 52.5 cm during the remainder of the experiments (observation intervals). As test salinities decreased so did the final depth distribution for given fish size ranges, except for 30- to 50-mm SL fish.

Changes in fish depth distribution were directly related to tank temperature, since water temperature decreased with depth. However, temperature values changed rapidly between depths 60 and 20-30 cm and were relatively isothermal and cold between 20-30 cm and the bottom of the tank, and isothermal and hot above 60 cm. As a result only small differences in final depth distribution corresponded with relatively large differences in final temperature distribution.

The mean selected temperature tended to increase between observation intervals 1 and 5 at each test salinity for given fish size ranges. The exception to this tendency was fish ≥50 mm SL at 0‰ salinity (20.9°-19.5°C). Fish ≤50 mm SL (20-30 and 30-50 mm) tended to select higher final observation interval 5) mean temperatures (30.0°-32.3°C) than did fish ≥50 mm SL (20.0°-19.5°C) at each test salinity. For all fish size ranges the final mean selected temperature tended to decrease as the test salinity decreased. This decrease was greatest for fish ≥50 mm SL (29.0°-19.5°C).

The depth and temperature distribution results taken together indicate that temperature selection was the more important, depth distribution being secondarily related. Other gradients such as light, pressure, and oxygen, if present, did not appear to influence the distribution of the mullet at least to the extent that temperature did. Fish ≤50 mm SL appeared to have a predilection towards the surface whereas fish ≥50 mm SL appeared to be predisposed towards the bottom. This was evident before the initiation of heating and chilling in each experiment and during constant temperature control experiments. As the experiments progressed it also appeared as if mullet ≤50 mm SL, in most instances, were "forced" downwards by rising temperatures. Similarly, mullet ≥50 mm SL were "forced" upwards by decreasing water temperature, and then downwards by rising temperature, such that their final temperature and depth distributions were somewhat lower than those for fish ≤50 mm SL in similar conditions.

Just how important the actual temperature and depth distribution values selected by mullet are is unknown. What does appear to be important is the relative difference between distributions for fish generally <50 mm SL as compared with those for fish generally >50 mm SL at each salinity, and the relative changes which occurred between salinities for each fish length interval. The predisposition of fish <50 mm SL towards the surface (and higher temperatures) may be adaptive in the field. Warm water rises and the warmest (hottest) water is usually on the surface. By moving in the surface layer fish <50 mm SL may be able to orient towards the shallowest water inshore, which at low tide should also be the warmest. The predisposition of fish >50 mm SL towards the bottom of the tank (and cooler temperatures) may similarly be adaptive in the field. In this case movement away from areas subjected to tide pool formation may be important for survival.

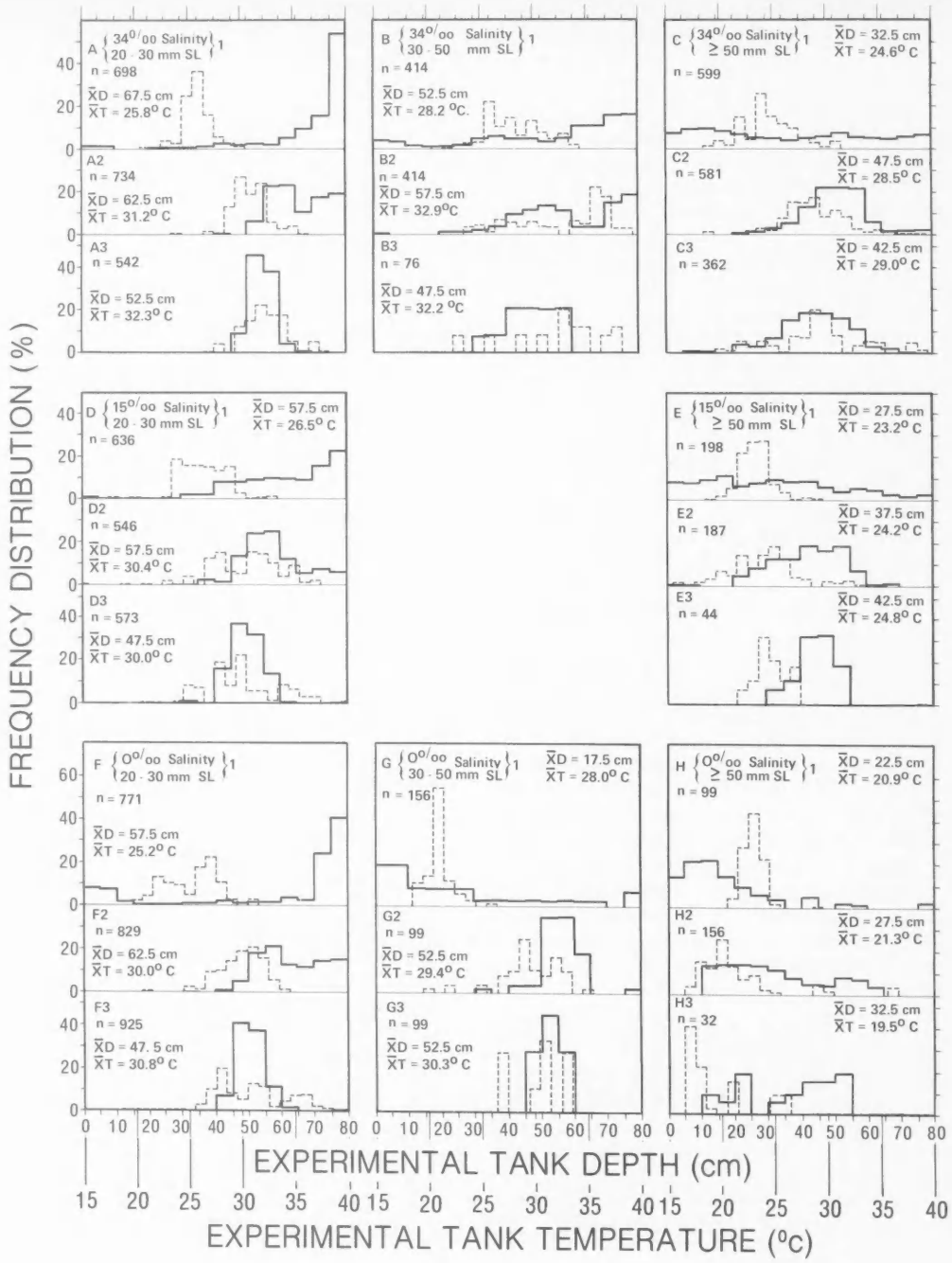

FREQUENCY DISTRIBUTION (%)
A {34°/oo Salinity, 20 - 30 mm SL} 1
n = 698
XD = 67.5 cm
XT = 25.8° C
A2
n = 734
XD = 62.5 cm
XT = 31.2° C
A3
n = 542
XD = 52.5 cm
XT = 32.3° C
B {34°/oo Salinity, 30 - 50 mm SL} 1
n = 414
XD = 52.5 cm
XT = 28.2 °C.
B2
n = 414
XD = 57.5 cm
XT = 32.9°C
B3
n = 76
XD = 47.5 cm
XT = 32.2 °C
C {34°/oo Salinity, ≥ 50 mm SL} 1
XD = 32.5 cm
XT = 24.6° C
n = 599
C2
n = 581
XD = 47.5 cm
XT = 28.5° C
C3
n = 362
XD = 42.5 cm
XT = 29.0° C
D {15°/oo Salinity, 20 - 30 mm SL} 1
XD = 57.5 cm
XT = 26.5° C
n = 636
D2
n = 546
XD = 57.5 cm
XT = 30.4° C
D3
n = 573
XD = 47.5 cm
XT = 30.0° C
E {15°/oo Salinity, ≥ 50 mm SL} 1
XD = 27.5 cm
XT = 23.2° C
n = 198
E2
n = 187
XD = 37.5 cm
XT = 24.2° C
E3
n = 44
XD = 42.5 cm
XT = 24.8° C
F {0°/oo Salinity, 20 - 30 mm SL} 1
n = 771
XD = 57.5 cm
XT = 25.2° C
F2
n = 829
XD = 62.5 cm
XT = 30.0° C
F3
n = 925
XD = 47. 5 cm
XT = 30.8° C
G {0°/oo Salinity, 30 - 50 mm SL} 1
XD = 17.5 cm
XT = 28.0° C
n = 156
G2
n = 99
XD = 52.5 cm
XT = 29.4° C
G3
n = 99
XD = 52.5 cm
XT = 30.3° C
H {0°/oo Salinity, ≥ 50 mm SL} 1
XD = 22.5 cm
XT = 20.9° C
n = 99
H2
n = 156
XD = 27.5 cm
XT = 21.3° C
H3
n = 32
XD = 32.5 cm
XT = 19.5° C
EXPERIMENTAL TANK DEPTH (cm)
EXPERIMENTAL TANK TEMPERATURE (°c)

FIGURE 3.—Experimental temperature (dashed line) and depth (solid line) distributions for indicated mullet size ranges in the 80-cm deep tank at the indicated salinity (34, 15, or 0‰). No experiments were conducted with fish 30-50 mm SL at 15‰ salinity. Each of the eight salinity-fish size range "conditions" are subdivided into three observation intervals: 1) observation interval 1, corresponding to the first three experimental observations (1-3); 2) observation interval 3 (7th-9th observations); and 3) interval 5 (13th-15th observations). Also presented are mean depth ($\bar{X}D$) and temperature ($\bar{X}T$) data. Sample size (n) is based on the pooled data for the number of times each fish was observed within the observation interval for all experiments at a given salinity and for a given fish size range. Experiments varied in duration and number of observations made. Thus, the sample size fluctuates. See Table 1 for the actual (maximum) number of fish and experiments for each salinity-fish size range condition.

Field

Mullet Distribution

The initial appearance of the 17- to 35-mm SL mullet prejuveniles, a distinct silvery, countershaded pelagic stage (Hubbs 1958), in the estuarine intertidal regions varied between 1972 and 1973. In 1972 they were observed and collected along the tide line (the most shoreward edge of falling or rising water, which is contiguous with deeper offshore water) in sand and mud flat tide pools and around freshwater streams and springs at the end of January. In 1973 they did not appear in these areas until the end of February. Prejuveniles were particularly abundant in areas with the finest silt, mud, and/or sand particles near the outlets of freshwater rivers, streams, or springs.

Fish ≥50 mm SL could be seen year around in the intertidal areas. The main body of this study concentrated on those fish that entered the intertidal in 1972. Also observed were juveniles of the 1971 year class, fish ≥80 mm SL, in the intertidal in early 1972, and prejuveniles and juveniles of the 1973 year class, ≤50 mm SL, in early 1973. The disappearance of prejuveniles-juveniles from the low tide intertidal swash zone (Hedgpeth 1957) and tide line regions appeared to be completed by the end of June each year, although occasional schools were seen as late as August. However, these schools were composed of fish usually about 40 mm SL or larger, that moved with the tide line.

Prejuvenile mullet undergo metamorphosis to juveniles after entering the estuarine intertidal region. The most evident change is the loss of the pelagic silvery coloration with a general darkening of all surfaces, especially the dorsal side. However, a general countershaded pattern remains. Other less obvious changes include: the elongation and convolution of the intestine, development of adipose eyelids, transformation of the third anal element from a soft ray to a spine, and changes in the morphology of lips and teeth. Metamorphosis is thought to be completed at about 50 mm SL (Jacot 1920).

During metamorphosis, diet and feeding habits change. I found copepods in the stomach contents of some prejuveniles in Hawaii in the estuarine intertidal regions. Other prejuveniles and juveniles had plant and animal material as well as mud or silt in their stomachs. I found that sediments constituted the bulk of the diet of juvenile mullet in some localities in Hawaii. In the estuarine intertidal region around the island of Oahu, the sizes of these injested particles ranged from 0.02 to 0.60 mm in diameter. Odum (1968) showed that fine particulate materials are a source of adsorbed organic matter and microorganisms, and are important in the diet of *Mugil cephalus* along parts of the east coast of the United States. The change in diet from copepods to plant material and mud or silt presumably occurs concurrently with changes in intestinal length, lips, and teeth. After metamorphosis is completed, the juvenile fish move into somewhat deeper intertidal water.

Prejuveniles and juveniles of all sizes formed schools ranging in size from tens to hundreds of individuals. Prejuveniles and juveniles <50 mm SL were always observed in the shallowest, warmest water near shore wherever they occurred (Table 2). At low tide they were located along the tide line, the shallowest water along estuarine streams, and trapped in shallow mud flat and occasionally sand tide pools (the swash zone). Intense continuous feeding activity was usually observed. The substrate in the areas in which the small mullet occurred was covered usually by the finest inorganic sediment (sand and silt 0.02-0.60 mm in diameter).

Salinity and temperature values changed daily depending on tide level (water depth), wind, bottom type (particle size, color, etc.), insolation, and the location of springs and streams. Often a spatial as well as temporal kaleidoscope of temperature and salinity values was recorded, especially along Wailupe Beach.

On 15 March 1972 the last hour (1200-1300 h local time) of a natural fish kill was observed in

TABLE 2.—Summary of field data collected during observations of prejuvenile and juveniles *Mugil cephalus* in Hawaii during 1972-73.

Locality	Habitat	Size (mm SL)	Month	Tide	Temperature range (°C)	Salinity range (‰)	Water depth (cm)	School size	Remarks
Wailupe Beach, Maunalua Bay[1]	Inshore of tide line in swash zone, tide pools, freshwater springs	<50	Feb. to May	Low	19.8-37.2 (22.0-26.9 in center of springs)	2-29.5	0.6-15	10's-100's	Mullet trapped in tide pools. No predators observed. No mullet ≥50 mm SL observed or collected.
	Coral rock/ rubble tide pools with open connections/channels to deeper water	≥50	Feb. to May; Dec.	Low	23.0-35.1 (22.0-26.9 in springs)	2-35 (2-10 in springs)	2.5-30	10's-100's	Seaward of tide line. Occasionally attacked by predatory fish.
	Mud/sand flats, sandy	<50	Feb. to June	High	26.1-30.1	10-35	5-30	10's-100's	In wave wash (tide line); attacked by predators.
	beach, coral rock/rubble	≥50	Feb. to June; Dec.	High	26.1-30.1	10-35	2.5-90	10's-100's	Feeding. Attacked by predators.
Wailupe Stream, Maunalua Bay[1]	Tidal stream	20-200	May	Low/ high	27.8	—	1.8-200	10's-100's	In shallowest water. Feeding during low tide. Attacked by predators at high tide.
Kaupa Pond, Maunalua Bay[1]	Cement drainage culverts	<50	Feb. to July	Low	21.9-36.2	0-32	0.6-13	10's	Tideline. Feeding in shallowest water.
	Mud bottomed channel	≥50	Feb. to July	Low	21.6-30.1	15-32	13-30+	10's	Feeding on surface. Unable to see below surface.
		<50	Feb. to July	High	28.1-34.0	15-32	0.6-13	10's	Along tide line—shallowest water.
		≥50	Feb. to July	High	28.1-34.0	15-32	30+	10's	Feeding.
Kahana Bay[1]	Silted areas, fishpond	<50	May	Low	—	—	0.6-5	10's	Feeding. No predators observed.
	Fishpond channels	30-200	May	Low	24.0-26.5	2-15	0.6-15+	10's	Feeding. No predators observed.
	River; mud/sand spits (bars)	<50	May	Low	24.1-29.6	2-30	0.6-5	10's	Feeding in tide line/shallowest water.
		≥50	May	Low	24.1-29.6	2-31	2.5-7.5	3-5	Feeding.
		<50	May	High	20.0-25.0	—	2.5-15	10's	Feeding in tide line/shallowest water amongst mangrove roots.
Kahana Bay[2]	River; mangrove vegetation	<50	May	Low/ high	—	—	2.5-15	—	In shallowest water. Individuals spread out motionless on bottom.
Wailupe Beach, Maunalua Bay[2]	Mudflats; coral rocks/ rubble	<50	Feb. to July	Low/ high	—	—	2.5-15	—	In shallowest water. Spread out or in compact groups motionless on bottom.
		≥50	Feb. to Aug.	Low/ high	—	—	7.5+	—	In shallowest water. Individuals spread out motionless on bottom.

[1]Daylight observations of mullet.
[2]Night observations of mullet.

one of the cement culverts in Kuapa Pond (Hawaii Kai), Maunalua Bay. The tide was low and just starting to turn and flood. Prior to this day heavy rains washed down large amounts of silt, rocks, and debris to a depth of about 0.2-0.5 m. A narrow channel was cut through the mud by the trickling stream, and isolated "tide pools" or pockets of water were common. An estimated several thousand prejuvenile and juvenile mullet 18-80 mm SL were found dead along the bottom of the culvert. Although it appeared that the fish had a free exit at higher tide levels, via the shallow (1 cm deep at low tide) channel to the cooler tidal region (26°-30°C), the fish were presumably trapped physically by the debris and/or by a very rapid increase in water temperature. Dead mullet were found in the pockets with water temperatures of 39.5°-42.5°C. The only survivors observed were mullet 20-35 mm SL slowly swimming in small pockets at temperatures as high as 39.0°-41.1°C. Salinity measurements were not made, but would be expected to be low.

Juvenile mullet ≥50 mm SL were not observed or collected in tide pools at low tide. At low tide these larger fish occurred beyond the tide line in tide pools with open connections to deeper water or along sills and sand/mud flats which sloped into deeper water. These areas were characterized by

higher but more uniform salinities and lower but more uniform temperatures than areas in which fish <50 mm SL were generally found.

At high tide, water temperature and salinity values were nearly uniform throughout a given location. Mullet <50 mm SL were concentrated along the tide line on the beach or along the sides of rivers in the shallowest water available. Schools were dense and often composed of more individuals than found in schools at low tide in the same area. Little feeding occurred; evasion of predators was seen more commonly. At high tide, schools of mullet with individuals ≥50 mm SL moved into the former tide line and tide pool areas, and were observed feeding in the areas from which the smaller mullet retreated.

The results of the experiments and field observations demonstrate that dynamic differences occur in the behavior and distribution of schools of mullet composed of individuals generally <50 mm SL as compared with schools with juveniles of greater length. In the field young mullet <50 mm SL prefer and select areas characterized by minimal water depth, tide pool formation, relatively high fluctuating temperatures, and relatively low fluctuating salinities. Juveniles ≥50 mm SL, on the other hand, seek somewhat deeper water and tide pools with lower more uniform temperatures and higher more uniform salinities.

Experimentally, a wide range of temperature values (13°-40.8°C) was available to the fish. However, mullet <50 mm SL tended to concentrate in water of higher temperature near the surface of the tank and fish >50 mm SL tended to occur deeper in the tank at lower temperatures for each test salinity. Although the experimental tank allowed fish a means of behaviorally escaping lethal or near lethal conditions (as presumably did deeper tide pools for mullet ≥50 mm SL in the field), entrapment in shallow intertidal tide pools in the field did not. Fish <50 mm SL appeared to actively seek such near lethal conditions in the field (and experimentally), and as observed in a Kuapa Pond stream culvert, occasionally perished as a result.

Predators

Most predators observed interacting with mullet during this study were solitary stalking or stationary "sit-and-wait" species (Table 3). Attacks by predators upon schools of mullet with individuals <50 mm SL were almost nonexistant at low tide.

Where deeper water was immediately contiguous with a shallow water shelf (e.g., along Kahana River), predators (e.g., barracuda) in the deeper water were observed orienting towards and paralleling the movements of schools of the small mullet feeding in the shallower water. When mullet strayed off the shelf into deeper water, they were attacked. Predation upon mullet ≥50 mm SL during low tide was occasionally observed as schools moved and fed in the deeper intertidal region.

At high tide, schools of these larger mullet continued to be attacked by predators, as they were at low tide. Similarly, during high tides and ebb and flood periods, predators attacked mullet schools with individuals <50 mm SL.

At night, along Wailupe Beach and the Kahana River (Table 2), mullet schools broke up and individuals spread out and remained relatively motionless near the bottom. The fish slowly moved

TABLE 3.—Predatory fish observed interacting with schools of mullet.

Location	Species	Standard length (mm)	Water depth (cm)	Tide	Remarks
Wailupe Beach	Lizardfish *Saurida gracilis*	60-175	5-23	Low/high	In tide pools with open connections and channels to deeper water. Attacked and chased juveniles of all sizes.
	Needlefish *Tylosurus crocodilus*	100-300	30-75	High	A possible predator, moved in with flood tide. Observed following schools of mullet near surface.
	Great barracuda, *Sphyraena barracuda*	50-225	30-75	Low/high	Moved inshore with flood tide; attacked and chased individuals of all sizes in schools. Followed feeding individuals in schools. Swam slowly along the shoreline at high tide.
Wailupe Stream	Great barracuda	40-600	30-90	Low/high	Mullet <50 mm SL usually in shallowest water 1.8-75 cm deep. Barracuda in deeper water followed or paralleled movements of mullet in shallow water and attacked when the mullet strayed into deeper water.
Hawaii Kai (Kuapa Pond) culverts	Great barracuda	30-250	15-75	High	Moved in with flood tide. Water turbid; caught in seines with juvenile mullet. No mullet found in stomach contents.
Kahana Bay River	Great barracuda	125-500	15-60	Low/high	At low tide mullet <50 mm SL in shallowest water 15 cm deep, barracuda followed (paralleled) schools of mullet in shallower water (see above).
	Eleotris sandwichensis	78	7.5-30	Low	Single unsuccessful attack on school of mullet of individuals about 40 mm SL. Caught after attack.

(drifted) with the tides. The break up of schools may have been a result of reduced predation and/or lowered visual sensitivity thresholds (Munz and MacFarland 1973).

When a school was attacked, it usually split into two or more segments and passed around behind the predator to reform a single school again. When a predator was successful in separating an individual from a school, a chase occurred, the results of which were seldom observed. Of the approximately 50 lizardfish stomach contents analyzed, one contained a juvenile mullet. None of the 10 barracuda stomach contents analyzed contained juvenile mullet.

Potential invertebrate predators were abundant in the various habitats where mullet occurred. However, only individuals of a single crab species, *Thalamita crenata*, were observed stalking and extending their chelipeds toward passing mullet. In one instance an individual crab did capture a juvenile mullet, but only after it had been wounded by and escaped from a barracuda.

DISCUSSION

Mugil cephalus is a worldwide (lat. 42°N-42°S, Thomson 1966) inhabitant of the estuarine intertidal as well as freshwater and coastal marine environments (Broadhead 1953, 1955; Hendricks 1961; Thomson 1963, 1966; Johnson and McClendon 1970). In Hawaii, selective pressures appear to have favored prejuvenile and juvenile mullet that are able to survive in the shallowest, warmest estuarine intertidal waters, waters that are characterized by temporal and spatial heterogeneity with respect to temperature, salinity, and depth. Before discussing the adaptations evolved by striped mullet making possible survival in estuarine intertidal regions, a discussion of the environmental variables important to young mullet in Hawaii might be in order.

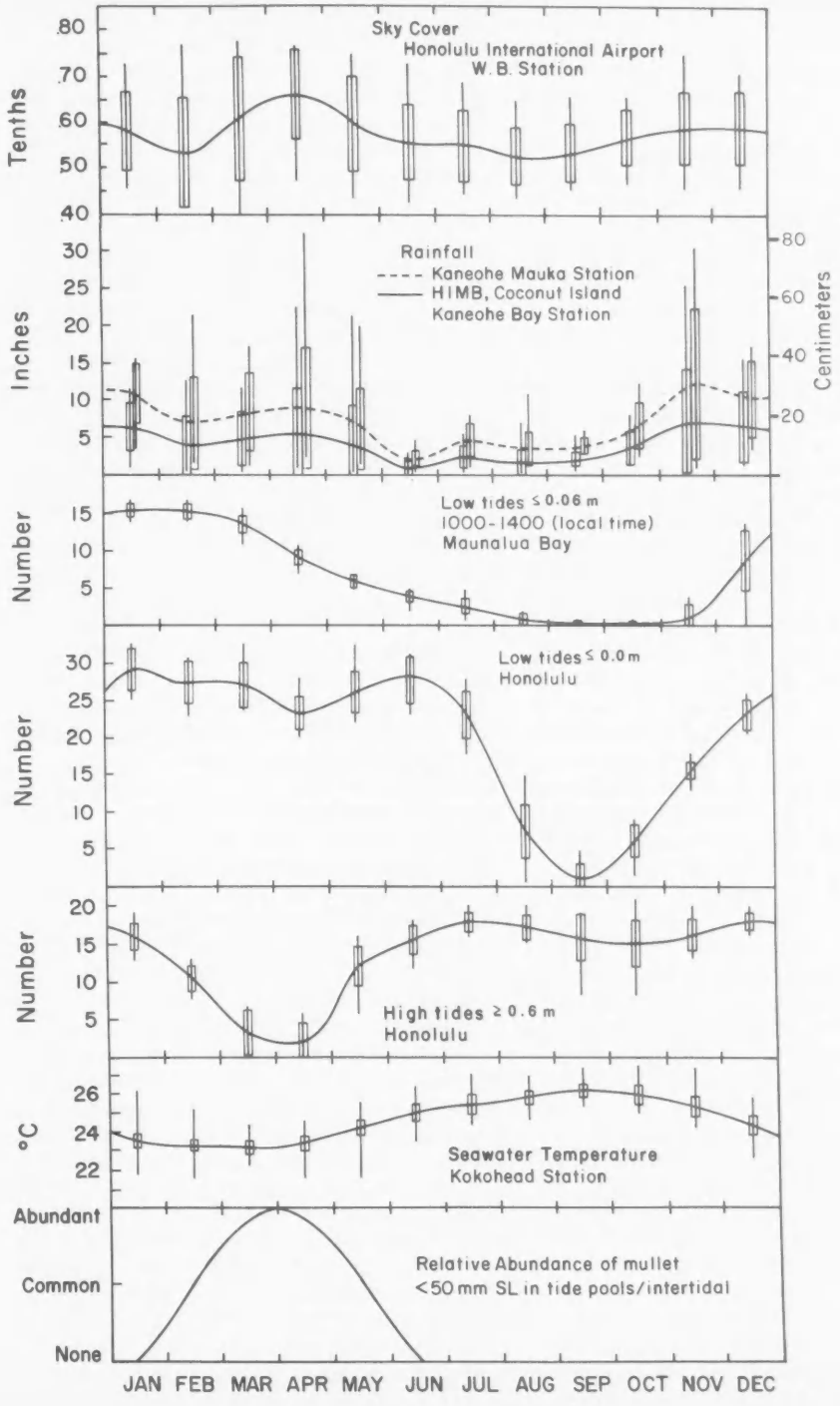
The monthly occurrence of mullet <50 mm SL observed in 1972 and 1973 in Hawaii is presented with data for 12 consecutive years (1962-73) of recorded (skycover, rainfall, seawater temperature) and predicted (tidal) data in Figure 4. These appear to be the most important environmental factors that bear directly upon the lives of mullet in the estuarine intertidal region. Indirectly, the length of daylight (time from sunrise to sunset) may also be important; it is shortest (about 10.9 h) about 22 December each year, and longest (13.3 h) about 21 June each year.

Visual observations and collections of mullet <50 mm SL indicate that these mullet occur in the Hawaiian intertidal estuarine regions during the months when there are a maximum number of low tides ≤0.0 m (mean tide level at Honolulu is 0.2 m (0.8 ft)). Perhaps of greater importance is the occurrence of mullet when there is a minimum number of high tides ≥0.6 m (2.0 ft). In Maunalua Bay, tide pools begin to form when the tide level is approximately 0.06 m (0.2 ft). The number of tides that would result in tide pool formation at noon (1000-1400 h local time) begins to decrease during the time of the year mullet are undergoing metamorphosis in the intertidal estuarine region, but is still maximal when prejuveniles first enter the inshore areas. Thermal and salinity stresses should be maximal during the noon time period. It is not known whether this tidal-estuarine intertidal situation is unique to Hawaii or of more wide spread occurrence. Also unknown is whether the peak occurrence of young mullet during such tidal relationships is fortuitous, or whether selection pressures have resulted in a shift of the peak occurrence from either earlier or later in the winter-spring season to its present "position" in April.

The extent to which stress occurs in the intertidal estuarine region may be ameliorated by low ambient (oceanic) seawater temperatures and maximum cloud cover. During the time mullet <50 mm SL are found in the intertidal estuarine region in Hawaii, seawater temperatures are minimal and increasing, and average cloud cover is seasonally maximal. During the late winter-spring, the lowest seasonal seawater temperatures occur in the tropical-temperate Northern Hemisphere, and increase until maximum levels are reached about September.

The average maximum amount of cloud cover, which occurs in Hawaii during April (when young

FIGURE 4.—The relative abundance of mullet <50 mm SL in the Hawaiian estuarine intertidal tide pools compared with environmental data collected (seawater temperature, rainfall, and sky cover) and predicted (tides). The monthly means (connected by horizontal lines), ranges (vertical lines), and standard deviations (vertical boxes) were derived from data for the 12-yr period, 1962-73. Mullet abundance data were from field observations and collections in 1972-73. Sky cover data were derived from monthly average values. Sky cover and rainfall data were taken from *Climatological Data, Hawaii*, U.S. Weather Bureau, NOAA; tidal information from *Tide Tables*, West Coast of North and South America including the Hawaiian Islands, National Ocean Survey, NOAA; seawater temperature data were collected by the National Marine Fisheries Service, Honolulu.


Sky Cover
Honolulu International Airport
W.B. Station
Tenths
80
70
60
50
40
Rainfall
Kaneohe Mauka Station
HIMB, Coconut Island
Kaneohe Bay Station
Inches
30
25
20
15
10
5
Centimeters
80
60
40
20
Low tides ≤ 0.06 m
1000-1400 (local time)
Maunalua Bay
Number
15
10
5
Low tides ≤ 0.0 m
Honolulu
Number
30
25
20
15
10
5
High tides ≥ 0.6 m
Honolulu
Number
20
15
10
5
Seawater Temperature
Kokohead Station
°C
26
24
22
Relative Abundance of mullet
<50 mm SL in tide pools/intertidal
Abundant
Common
None
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC

mullet are most abundant), reduces insolation and thus reduces the potential for the attainment of lethal conditions in tide pools. These relationships are particularly important since young mullet congregate in areas of springs and freshwater run-off. However, cloud cover during February through May varies more than during any other period of the year and points to the fact that the environment in which mullet <50 mm SL occur fluctuates tremendously within a season and from year to year.

Seasonal rainfall is maximal during winter-spring in Hawaii. Rainfall in the mountains (Kaneohe Mauka Station) exceeds that in nearby shore regions (Hawaii Institute of Marine Biology Station). Fluctuations in rainfall from month to month and year to year are great and appear to be unpredictable, particularly during the season when mullet <50 mm SL are abundant in the intertidal estuarine region. Run-off is maximal during this season due to the heavier mountain rainfall. This run-off could contribute to potentially lethal or near lethal conditions in the intertidal region by reducing its salinity, particularly during periods when low tides occur during noon. Intertidal spring water temperatures, on the other hand, were recorded to be as much as 10° cooler than surrounding water of higher salinity (Table 2). This cooler water may serve to reduce overall intertidal estuarine temperatures, at least during nontide-pool forming tide levels, but at the same time it increases the thermal and salinity heterogeneity of the environment.

Returning to a discussion of adaptations of mullet, experimental studies indicate that temperature acclimation is important in the ability of striped mullet (at least larger juveniles) to survive higher temperatures (Heath 1967; Sylvester 1974, 1975; Sylvester et al. 1974). Heath, although not providing fish length or salinity data at which tests were made, reported critical thermal maxima (CTM) of 42.4°-43.1°C for mullet in the northern Gulf of California. Sylvester (1974, 1975) and Sylvester et al. (1974) demonstrated increased CTM (29.0°-41.6°C) with increasing acclimation temperatures at a salinity of 32‰ for juvenile striped mullet, 70-125 mm SL, in Hawaii. At a lower acclimation temperature, and a salinity of 0‰, the CTM's were reduced. In general, CTM's were lower at lower salinities. Sylvester (1974) also found that juveniles adjusted or acclimated faster at higher temperatures, and that their thermal resistance to lethal temperatures decreased slightly when they were exposed to fluctuating low, rather than constant, temperatures.

Sylvester (1975) also demonstrated the existence of increased CTM at noon and lower CTM in the morning and afternoon for fish 78-122 mm SL.

There is good evidence that underlying biochemical changes are responsible for acclimation to changing thermal regimes (reviews in Hochachka and Somero 1971, 1973; Haschemeyer 1973; Somero 1975). Hochachka and Clayton-Hochachka (1973) provided some evidence that this may also be the case for striped mullet about 120 mm long in Hawaii.

Whether the ability of mullet to tolerate increasingly higher temperatures, seasonally and daily, is a result of interacting endogenous factors (biological rhythms) as is indicated in other animals (Sweeney and Hastings 1960; Wilkins 1965), and/or exogenous factors (direct exposure to increasing temperatures) is not known.

Sylvester's (1974, 1975) studies were conducted between August and January and those of Heath (1967) in March and September. As the discussion above and Figure 4 indicate, ambient seawater temperatures are highest during August to October and lowest during February to April in the tropical-temperate Northern Hemisphere. Although the seasons varied during which the experiments of Sylvester and Heath were conducted, the CTM data obtained were similar for the experimentally acclimated fish. Doudoroff (1957) and Allen and Strawn (1971) reported that relatively brief exposure to high nonlethal temperatures usually increased heat resistance in a number of species of fish. This increased resistance was not readily lost when fishes were subsequently exposed to low temperatures. This also appears to be true for striped mullet as Sylvester's (1974) study indicates. Thus, striped mullet appear to have an ability to modify their thermal tolerance in direct response to prevailing environmental conditions (exogenous factors). The ability to increase their heat resistance even after a brief exposure to high nonlethal temperature would be especially advantageous to mullet in the estuarine intertidal, at least in Hawaii.

If exogenous factors are solely responsible for the ability of striped mullet to survive high temperatures, it is difficult to explain the differences in the distribution of striped mullet presented in this report.

Prejuveniles enter the intertidal estuarine regions from the far more environmentally uniform

oceanic waters, and appear to be "preadapted" to the near lethal conditions inshore. This may indicate the existence of an ontogenetic biological rhythm (cued by slight monthly changes in photoperiod or water temperature?) in these mullet, which biochemically and physiologically preadapts these fish for life in the intertidal estuarine regions, while they are still in oceanic waters. Seasonal and daily acclimation to existing thermal and salinity regimes may then occur after the prejuveniles arrive inshore.

Factors affecting the distribution of striped mullet ≥50 mm SL are more complex. In Hawaii, field acclimated fish behaviorally select or prefer water temperatures well below their experimental CTM. The natural fish kill observed in March also indicates that the larger juveniles (and most prejuveniles) were not able to survive exposure to high temperatures (at least for relatively long periods of time). Behavioral selection of temperature regimes well below CTM has also been observed in the estuarine goby, *Gillichthys mirabilis* (de Vlaming 1971).

Mullet ≥50 mm SL in Hawaii moved seaward to pools with open connections to deeper water with ebbing tides during the spring. During the nontide-pool forming low tides in the late summer, the larger juveniles may be acclimated to tolerate higher ambient seawater temperatures in Hawaii as they are in the northern Gulf of California. In Hawaii, however, intertidal waters reach their maximum temperatures during the period from late winter to early summer when shallow tide pools are formed, although ambient oceanic temperatures are higher during late summer. Heath (1967) indicated that inshore water temperatures in the northern Gulf of California are highest during the late summer-early fall period. It is not known whether CTM's are similar for field acclimated striped mullet ≥50 mm SL in the spring in Hawaii and in the late summer in the northern Gulf of California, or whether mullet from both locations have CTM's parallelling seasonal changes in ambient (oceanic) seawater temperature.

Selected temperatures are lower for young mullet ≥50 mm SL compared with smaller fish at each salinity, and much lower at decreasingly lower salinities (Figure 3). Presumably, physiological changes mediated hormonally/biochemically occur during metamorphosis, resulting in a preference for reduced temperatures by the larger juveniles. This decrease in temperature "tolerance" with metamorphosis (age) is somewhat contrary to the discussion thus far. It may only be a behavioral trait not directly correlated with CTM (i.e., CTM may actually be increasing). Behavioral selection of lower temperatures appears to be adaptive in the field during the period between April and August. In addition to having widely varying salinity values, many of the tide pools formed during this period may have been too shallow for larger juveniles to feed and swim. Many of the pools were shallower than the body depth of the older juveniles. Thus, those individuals that remained seaward of the tide line as they completed metamorphosis may have reduced or escaped the possibility of entrapment and exposure to lethal conditions in tide pools and shallow water; conditions observed once during this study.

These relationships may indicate the existence of an endogenous rhythm involved in the movement of (behavioral selection by) juvenile mullet towards deeper, relatively cooler, more saline water during or after metamorphosis. This rhythm may be acting in opposition to the presumably increased acclimation to higher ambient (oceanic) seawater temperatures. The change in behavior with metamorphosis may be a result of endogenous rhythms perhaps coupled with exogenous factors, such as the slight monthly changes occurring in seawater temperature and/or photoperiod, or it may be due directly to these exogenous factors. The reproductive cycle of striped mullet appears to be coupled with both these environmental variables (Kuo et al. 1974; Kuo and Nash 1975), so presumably younger individuals could use these same cues as well. It is difficult to separate cause from effect, but the shallowness and volume limitations of tide pools may be critical. Thus, selection may have favored those metamorphosed individuals with reduced physiological tolerance to high fluctuating temperatures and low fluctuating salinities as found in the estuarine intertidal (i.e., those individuals that behaviorally moved away from such conditions).

If selection favored those metamorphosed (metamorphosing) individuals that moved into deeper intertidal waters, what selection pressures may have favored individuals able to survive the kaleidoscopic conditions of the estuarine intertidal tide pools?

Experimental and field evidence demonstrate the importance of refugia for species from their competitors and/or predators (Gause 1934; Crombie 1946; Connell 1961; Paine 1969). Connell

proposed that intertidal species are limited in their upper distributional range by physiological (and presumably biochemical) adaptive abilities to environmental stress. At the lower end of the range, organisms are limited by biotic factors such as competition and predation. Field observations indicated that there was essentially no predation, including that by birds, of mullet <50 mm SL when they occupied the intertidal estuarine tide line and swash zone areas at low tide (Tables 2, 3). At high tide, and during ebb and flood, mullet <50 mm SL were exposed to predators, but the potential for being attacked and caught was reduced by occupying the shallowest tide line waters and by the schooling habit.

The absence of predatory fishes in the shallow intertidal estuarine regions at low tide may be related to 1) a subminimal depth or area of water in which to maneuver, and 2) possibly, although data are lacking, an inability of predators to adjust to rapidly fluctuating thermal and salinity regimes. Predators escaped entrapment by remaining seaward of the tide line during ebbing tides just as juvenile mullet ≥50 mm SL did. In addition, potential invertebrate predators were absent from the shallow intertidal areas presumably escaping seaward and/or, as often observed or caught, burrowing to a level below the surface of the mud/sand substrate.

Juvenile mullet ≥50 mm SL as well as adult mullet appear to be competitors with individuals <50 mm SL for food resources in the intertidal estuarine region. At high tides the larger fish moved into and fed in the areas used by the younger fish during low tides. With the incoming tide, the younger fish moved shoreward with the tide line. In addition, other species of fishes moved in with the flood tides. It is not known whether these fishes utilized the same food resources as the young mullet.

Space also may be at a premium in the shallow intertidal estuarine regions, particularly in tide pools. As discussed previously, the volume of water in the tide pools as well as the depth of pool water may be critical. Formation of large schools is characteristic of larger juvenile mullet as it is for the species as a whole and inter- and intraspecific competition for space may occur. Other species of fishes, as well as the larger juvenile mullet, were not observed in the shallowest water during low tide. The ability of small mullet to occupy the shallowest, warmest water may also occur in the northern Gulf of California (Heath 1967), where they (no length data) are one of two species penetrating the farthest up seawater drainages along the margin of the desert.

Mullet <50 mm SL formed loose schools with individuals constantly feeding during low tides, particularly in tide pools. At high tides, or in more exposed environments, feeding often ceased and tight dense schools were formed. This was evident when predators were nearby, approaching, or attacking. When exposed to predators at high tides and changing tides, the schooling habit confers an increased advantage to the mullet in terms of survival (Major 1977, in press). Most of the attacks by predators on schools that I observed, failed. The formation of schools appears to be yet another adaptive feature in the behavioral repertory of mullet. The schooling habit increases the ability of individual mullet to survive as prejuvenile and juveniles in the intertidal estuarine region and presumably as prejuveniles in oceanic waters.

Prejuvenile and small juvenile mullet have presumably evolved the necessary biochemical and physiological adaptations to exist successfully in the fluctuating, often near lethal, intertidal estuarine environment in the spring months. In Hawaii, this has allowed them to use this intertidal refugium to escape their predators and competitors for food and space, making possible undisturbed feeding activity. Kinne's (1960) work with *Cyprinodon macularius* and Norris's (1963) study of *Girella nigricans* suggest that high temperatures increase the rate of food uptake and digestion. Food conversion (to growth) efficiencies are highest at lower temperatures, however. De Silva and Perera (1976) experimentally determined that young mullet grow more rapidly at 20‰ salinity than at salinities of 30, 10, or 1‰. This was comparable to Kinne's (1960) work with *C. macularius*.

The widely fluctuating environmental variables in the estuarine intertidal in Hawaii may provide the necessary conditions for rapid growth in mullet. This would allow metamorphosis to be completed in all mullet by the time the tidal situation becomes less favorable, as predators gain access to the small mullet and intra- and interspecific competitors gain access to their feeding areas as well. The formation of large schools during all stages of life appears to be important in reducing predation and possibly also in competing with other species for food and space in the estuarine intertidal region.

It is interesting to note that the environmental conditions and the behavior of prejuveniles and juvenile striped mullet in Hawaii appear to be very similar in many instances to those of various species of western U.S. desert pupfish, *Cyprinodon* (Barlow 1958, 1961; Kinne 1960; Lowe and Heath 1969; Brown and Feldmeth 1971; Deacon and Minckley 1974), and to the African cichlid, *Tilapia grahami* (Coe 1966). Daily and seasonal changes in water temperature and possibly salinity (ionic) regimes in the low tide, tide pools in Hawaii and desert springs and pools appear very similar. The pupfish and *T. grahami* young live in the shallowest, hottest water often at near lethal temperatures. Adults, generally, did not occur in these areas at the same time as the young. Feeding appeared to be continuous and was directed at the substrate, as it was in mullet <50 mm SL. The shape, size, and length of the pupfish and *T. grahami* also appear to be very similar to those of the small mullet.

The changes occurring in the behavior and distribution of mullet prejuveniles transforming to juveniles is also very similar to the changes occurring in prejuvenile and juveniles opaleye, *Girella, nigricans,* in the intertidal areas along southern California and Baja California, Mexico (Norris 1963).

The ability of certain life history stages of these diverse species of fishes to tolerate fluctuating conditions and/or near lethal thermal and ionic (salinity) regimes in shallow water possibly indicates convergence of adaptations to similar environments. The physiological adaptations may be mediated biochemically (hormonally) and may be a result of the interaction of both endogenous and exogenous factors or cues. The evolutionary driving or selection forces operating appear to include predation and at least intraspecific competition for food and space.

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AGING OF GULF MENHADEN, *BREVOORTIA PATRONUS*

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ABSTRACT

Length-frequency distributions, returns of tagged juveniles, and scale annuli indicate that over 97% of Gulf menhaden, *Brevoortia patronus*, caught in the purse seine fishery are ages 1 and 2. Few fish survive to age 3. About 50% of the fish examined for the years 1971-73 could be aged by scale annuli. Those with no scale annuli or with indistinct or false annuli could be assigned to age 1 or younger or age 2 or older on the basis of length.

When large numbers of fish are routinely sampled for age and size distributions, they must be aged by some technique that consumes relatively little time. One common method is to count scale annuli, another is to group the fish by length frequencies. Counting otolith rings usually is impractical because of the large amount of time and effort it takes to collect, prepare, and observe the otoliths.

As pointed out by Struhsaker and Uchiyama (1976), "Attempts to age tropical fishes by conventional methods have generally been thwarted by the absence of well-defined annuli in calcarious structures and protracted spawning periods which make length-frequency mode progression analysis difficult." In temperate regions where the winter water temperature may not fall low enough to cause a cessation of fish growth for an extended period, aging fish by counting scale annuli may also be difficult.

Gulf menhaden, *Brevoortia patronus*, range along the coasts of the United States and Mexico from Florida to Yucatan. They spawn offshore in the Gulf of Mexico from about October to April (Suttkus 1956; Turner 1969). The eggs hatch in about 48 h and the larvae are transported by onshore currents to estuaries, where they metamorphose into adult form (Fore and Baxter 1972). In late summer the juveniles, ranging from about 45 to 120 mm fork length (FL), congregate in the lower estuaries before moving to offshore waters (Kroger and Pristas 1975).

Gulf menhaden, the basic resource for a large meal and oil industry, are caught exclusively in a purse seine fishery extending from western Florida to eastern Texas. Processing plants, now operating only in Mississippi and Louisiana, formerly operated in Florida and Texas also. During routine sampling of the catch during the fishing season, usually lasting from late April to October, scales have been removed from, and weights and fork lengths recorded for, about 13,000 fish annually since 1964.

Aging these fish by conventional methods has been a problem. Although some fish had well-defined rings that appeared to be annuli, others had no rings, or rings that were unclear or oddly spaced. Length-frequency distributions indicated two major age-groups with overlapping lengths, and a third group that appeared in late summer.

Since neither length frequencies nor scale rings alone were satisfactory for aging all fish, ages subsequently were based on a combination of factors: appearance of scales, number and spacing of visible rings, and length of fish at the time it was caught. This method of aging could be criticized as being too subjective. But until returns of fish tagged at a known age, such as juveniles, were available there were no distributions of known ages to which distributions of estimated ages based on scale rings and lengths could be compared.

A study to resolve the problem was not begun until returns of juveniles tagged in late summer and early fall 1970-73 became available. In 1975 we began a study of fish collected from 1971 to 1973. We choose those years because returns of tagged juveniles of the 1970-73 year classes were available, and we limited our material to 3 yr to keep it manageable. Age-0 fish were defined as young-of-the-year that would have no scale ring, age 1 as those in their second year that should have one ring, and age 2 as those in their third year that should have two rings.

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Our primary objective was to determine if rings visible on some scales were true annuli. If they were, our second objective was to determine if fish that had scales with no visible rings or with a profusion of unclear rings could be aged on the basis of length; if the rings were not annuli, our second objective was to explore other methods of aging Gulf menhaden.

COLLECTION OF DATA

Samples of the catch are taken daily by field personnel stationed at four ports, each comprising two or three plants grouped in close proximity. After weighing and measuring a fish, samplers remove a cluster of scales from just above the lateral line below the dorsal fin and deposit them in a 0.1% phenol solution. Later, six scales from each fish are cleaned and mounted between two glass slides. Each fish and its scales are identified by port, collection, and scale number. From 1964 to 1971, two samples of 20 fish each were taken daily at each port. Since 1972, three samples of 10 fish each have been taken.

Juveniles ranging from about 80 to 120 mm FL were marked in late summer and early autumn with numbered internal ferro magnetic tags similar to, but smaller than, those used for adults (Pristas and Willis 1973). Tags were recovered on magnets in various parts of the processing plants (Parker 1973), although all tags passing through a plant were not retained.

To estimate the numbers of field tags not retained on magnets, batches of 100 fish marked with test tags were periodically planted in the catches. The percentage subsequently recovered was an estimate of the efficiency of the magents to recover field tags. The number of annual tests at each plant varied from 2 to 15 (200-1,500 tags). Annual recovery rates varied from 2 to 60%, but over one-half were between 15 and 40%.

Some test tags were not recovered until 1, 2, or even 3 yr after they had been placed in catches (Table 1). Delayed recoveries were caused by 1) tags lodging in various parts of a plant before later being dislodged, 2) tags remaining in fish scrap stored for long periods before being ground, 3) tags remaining in various scrap storage areas before being mixed with new scrap. The number varied by plant and year and amounted to about 1% or less of the number of test tags applied, although in 1972 it was 6% at plant 58 and 5% at plant 57.

TABLE 1.—Number of test tags applied and number recovered at Gulf menhaden processing plants, 1971-73.

Plant no.	Year tags applied	No. of tags	No. recovered			
			1971	1972	1973	1974
54	1971	900	28	0	(1)	(1)
	1972	1,300		703	(1)	(1)
55	1971	900	100	4	6	0
	1972	1,400		598	13	0
	1973	700			255	7
56	1971	900	448	0	1	1
	1972	1,300		617	2	0
	1973	600			199	2
57	1971	200	40	1	1	0
	1972	1,300		301	59	3
	1973	1,200			322	7
58	1971	300	43	5	0	0
	1972	1,500		425	93	0
	1973	1,200			396	3
62	1971	1,200	470	1	0	0
	1972	1,300		654	1	0
	1973	1,100			658	2
63	1971	1,000	203	12	0	0
	1972	1,000		379	8	0
	1973	1,200			217	13
64	1971	930	395	8	0	0
	1972	1,200		314	4	0
	1973	1,100			241	6
65	1971	800	399	(2)	(2)	(2)
68	1971	1,100	436	2	0	0
	1972	900		311	12	0
	1973	400			214	0
69	1971	1,000	163	1	0	0
	1972	1,100		265	3	0
	1973	1,300			273	1
71	1971	1,100	205	0	1	0
	1972	1,100		317	0	0
	1973	1,200			186	0

[1]Plant did not operate after 1972.
[2]Plant did not operate after 1971.

OBSERVATION OF SCALES

Scales were viewed on a scale projector at 48× magnification. If no rings were evident, or if no one ring could be considered as an annulus, no measurements were made. If rings were evident, the distances from the focus to each ring and to the scale edge of the projected image were measured. Each ring had to be discernable on three or more scales or it was not measured. Each fish was assigned an age corresponding to the number of rings on the scales except when the only ring visible was in the area of the scale usually occupied by the second ring. Then the fish was called age 2 rather than age 1. The decision to assign a ring the number one or two position was based on the distance of the ring from the scale focus.

VALIDITY OF RINGS AS YEAR MARKS

To determine if observed rings were true annuli, we examined three different sets of data: length-

frequency distributions of sampled fish, returns of tagged juvenile menhaden, and spacing of rings on the scales.

Length-Frequency Distributions

From the general shape and the number of modes of a length-frequency distribution curve, it is often possible to infer the number of age-groups represented. Length-frequency curves of Gulf menhaden sampled during 1964-73 fishing seasons had two distinct modes. Since distributions in all years were similar, we have shown only those for 1967-70 (Figure 1). A prominent mode, usually evident in May at around 135 to 150 mm, shifted progressively to the right during the season and by September varied from about 155 to 170 mm. A smaller mode at about 170 to 180 mm in May tended to shift farther right during the season and disappear by midsummer, so that the curve became unimodal and greatly skewed. This small mode apparent in May appeared to be a continuation of the mode that was prominant during the preceding September.

From the general shape of the length-frequency curves there appears to be only two dominant age-groups in the fishery. The younger and more numerous tends to dominate the fishery as the

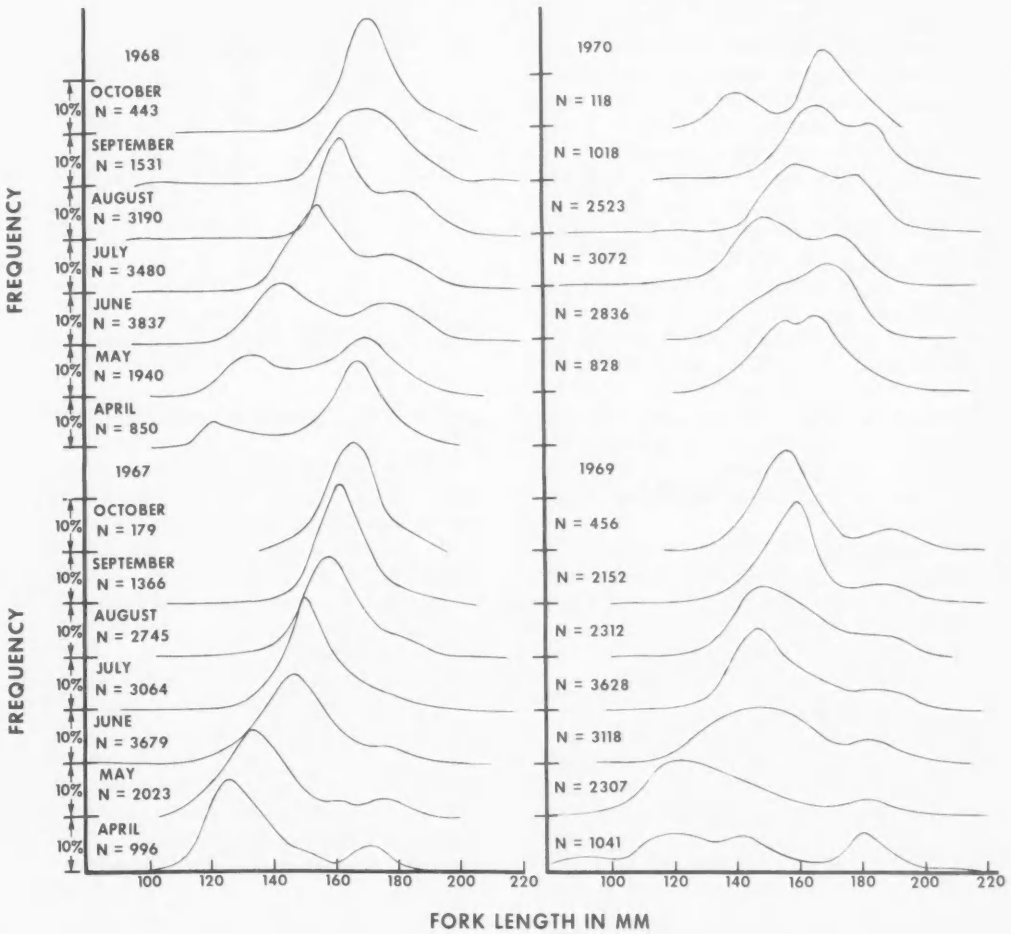

FIGURE 1.—Length-frequency distributions of Gulf menhaden in percent, by month, 1967-70.

season advances, so that by the end of the season the catch is composed almost entirely of this age-group. The considerable variation in the relative numbers of the two major age-groups from year to year is probably a reflection of the differences in the relative abundance of each year class. Small numbers of a third age-group of still younger fish may enter the fishery in some years in August or September.

Juvenile Tagging

An advantage of tagging juveniles is that the age of each fish is known when it is recaptured. Unfortunately, recovery of some tags a year or more after they had entered a plant caused some fish to appear older at the time of recapture than they actually were. Although the number was relatively small, it had an important bearing on inferences pertaining to longevity and the proportion of older fish in the catch.

By the end of the 1974 fishing season 1,137 field tags had been recovered (Table 2). Of these 1,069 (94.0%) were recovered in the 2 yr following tagging, 62 (5.5%) in the third year, and 6 (0.5%) in the fourth year. Only tags applied in 1970 had an opportunity to be recovered in the fourth year, and only tags applied in 1970 and 1971 had an opportunity to be recovered in the third year.

The tendency for test tags to remain in plants for one or more years leads us to believe that all field tags recovered in the fourth year and most of those recovered in the third year were holdovers from previous years. All of these tags were recovered at plants that had the highest percentage of test tag holdovers.

We conclude, therefore, that at least 97% of Gulf menhaden caught in the purse seine fishery are age 1 or age 2, and that very few, probably less than 1%—live to age 3. If ring marks are valid annuli, they also should indicate that the catch is composed primarily of age-1 and age-2 fish.

Incidence and Spacing of Scale Rings

The scale length-fish length relation for Gulf menhaden was linear. Correlation coefficients for 1971, 1972, and 1973, based on fish ranging from 95 to 225 mm FL, was 0.790, 0.765, and 0.768, respectively; for log transformed data the coefficients decreased to 0.729, 0.695, and 0.681. Sample sizes were 4,674, 4,457, and 4,902, respectively. The regression equation for the 3 yr combined was: Scale length = 5.392 + 0.865 Fish length.

TABLE 2.—Numbers of field tags of juvenile Gulf menhaden recovered from 10,458 fish tagged in 1970, 15,511 in 1971, 15,262 in 1972, by plant.

Plant no.	Year tagged	No. recovered			
		1971	1972	1973	1974
54	1970	2	30	(1)	(1)
	1971		5	(1)	(1)
55	1970	16	3	3	1
	1971		14	31	5
	1972			76	35
56	1970	29	30	3	2
	1971		10	33	7
	1972			54	30
57	1970	5	5	4	0
	1971		4	14	2
	1972			16	3
58	1970	2	19	18	1
	1971		2	24	6
	1972			6	12
62	1970	0	3	1	1
	1971		18	13	2
	1972			12	17
63	1970	3	2	0	0
	1971		49	2	1
	1972			28	4
64	1970	19	0	0	0
	1971		95	1	1
	1972			54	1
65	1970	7	(2)	(2)	(2)
68	1970	3	7	3	0
	1971		45	16	2
	1972			36	17
69	1970	1	7	2	1
	1971		5	7	1
	1972			9	6
71	1970	4	2	0	0
	1971		43	1	1
	1972			21	1

[1]Plant did not operate after 1972.
[2]Plant did not operate after 1971.

Not all fish had scales with clearly discernable rings. The percentage with no rings varied from 45.0 to 55.8. Of the fish considered as age 2, <2% had a ring in the number one position only and 25.1% in 1971, 39.1% in 1972, and 30.6% in 1973 had a ring in the second position only. A relatively small number of fish had scales with three clearly discernable rings.

The length frequencies from May to September of fish with one or two rings clearly indicated two distinct ages. In Tables 3-5 length groups below the first containing fish with both one and two rings have been lumped into one group. For one-ring fish the mode is the group, other than the lumped one, containing the most fish. The only exception is for May 1971 when the mode for fish with one ring was 155 mm. It is clear that the modes and means of one- and two-ring fish increased and that the distributions shifted toward larger sizes as the season progressed.

TABLE 3.—Length frequencies and mean lengths of Gulf Menhaden, by month and number of scale rings (0-3), 1971.

Fork length (mm)	May				June				July				August				September			
	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3
<165	50	150			560	747			587	503			663	330			260	48		
165-169	1	14			31	99	3		36	80	1		74	61			55	17		
170-174	4	14	6		45	74	16		32	95	1		49	69	1		29	22		
175-179	14	6	9		67	42	56		41	69	27		28	76	2		19	18	4	
180-184	11		22		84	18	111		53	43	100		44	61	6		27	19	10	
185-189	12		26		78	2	134		56	14	108	1	36	32	32		15	5	15	
190-194	4		29		53		83	3	42		144	5	44	15	48	2	22	6	17	
195-199	3		10	1	30		49	7	29		68	2	28	1	52	3	10	2	9	1
200-204	3		4	2	18		14	3	14		35	17	16		35	5	11		4	1
205-209				1	1		6	1	2		11	7	4		6	4	1		4	2
210-214	1				2		1	4				8	5		3	5	2		1	3
215-219								1				2	1			2	1			2
220-224	1							1												
Total number	104	184	106	4	969	982	473	20	892	804	495	42	992	645	185	21	452	137	54	9
Mean length	—	148	187	202	—	154	186	202	—	160	189	203	—	165	194	204	—	169	191	209

TABLE 4.—Length frequencies and mean lengths of Gulf menhaden, by month and number of scale rings (0-3), 1972.

Fork length (mm)	May				June				July				August				September			
	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3
<155	288	353			264	338			198	102			97	39			41	6		
155-159	64	79	3		158	134			204	107			136	51			14	7		
160-164	109	94	5		170	114	1		339	169			280	129			47	11		
165-169	109	75	12		192	88	3		236	126			347	134	1		33	19		
170-174	79	47	52		120	99	24		178	78	9		180	83	3		43	10		
175-179	53	5	71		86	48	42		136	54	39		118	54	7		57	14		
180-184	44	1	72		45	7	59		97	41	52		102	33	24		44	7	1	
185-189	20		55	1	36		72		70	6	102		78	8	74		28	1	1	
190-194	16		27	2	17		66	2	37	1	89	2	79	3	105		25	1	5	
195-199	7		13	7	15		31	3	42		79	3	65		77		17		8	
200-204	8		4	4	11		12	4	19		40	3	30		46	3	26		1	
205-209	2			2	4		3	4	16		20	4	19		10	4	10		1	
210-214				1	9		2	9	13		10	7	9		5	3	7			
215-219					3			4	5		1	3	7		1	3	1			
220-224				1	1				2		1	3	2		1	8	1			
225-229								1	1		1	1	1			1				
Total number	799	654	314	18	1,131	826	315	27	1,593	694	443	26	1,550	534	354	22	394	76	17	
Mean length	—	151	181	198	—	157	186	208	—	164	191	209	—	166	193	215	—	170	194	

TABLE 5.—Length frequencies and mean lengths of Gulf menhaden by month and scale rings (0-3), 1973.

Fork length (mm)	May				June				July				August				September			
	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3	0	1	2	3
<155	162	55			265	109			181	41			171	10			49	2		
155-159	80	28	1		217	105			187	103			26	22			1			
160-164	94	17	13		151	117			229	190			77	71			2	1		
165-169	69	16	27		93	80	2		210	169			127	164			11	12		
170-174	44	16	45		96	79	14		204	207	2		138	295			16	26		
175-179	40	4	44		90	39	70		150	138	24		237	100	3		34	26	3	
180-184	21		42		68	11	169		95	89	73		143	71	32		31	28	7	
185-189	6		30		28	5	196		82	43	114		75	35	80		19	16	12	
190-194	7		26	1	16	1	119		34	19	117		50	12	88		15	3	28	
195-199	4		12		15		71	3	15	1	81		14	1	64		17	2	16	
200-204	1		12	1	10		46	6	10		49	4	14		42	6	8	1	16	2
205-209	1		4	2	2		28	2	7		26	3	8		28		5		5	1
210-214	3		4	4	8		13	8	5		12	5	5		8	6	9			
215-219				3	2		1	5	1		6	3	2		2	8	2			2
220-224					1			5	1		2	3	4		1	4	3			2
225-229								2	1			2	1			2	1			
Total number	532	136	260	11	1,062	546	729	31	1,412	1,000	506	20	1,092	781	348	26	223	117	87	7
Mean length	—	158	182	210	—	162	188	211	—	169	192	213	—	172	194	214	—	178	193	211

TABLE 6.—Mean distance from last ring to scale edge expressed as the percent of the distance from focus to scale edge for Gulf menhaden.

Period	1971			1972			1973		
	Age 1	Age 2	Age 3	Age 1	Age 2	Age 3	Age 1	Age 2	Age 3
1-15 May	36.7	9.9	5.0	24.6	11.6	—	29.6	13.3	6.7
16-31 May	37.0	10.6	—	35.8	12.5	5.2	32.6	15.2	7.3
1-15 June	40.1	12.4	7.7	39.1	13.8	5.7	34.8	17.4	8.8
16-30 June	42.1	12.6	7.3	39.9	15.6	5.8	38.0	18.9	8.7
1-15 July	43.2	13.0	7.4	42.1	15.7	6.7	40.4	20.7	8.6
16-31 July	43.5	12.7	7.4	41.6	15.0	6.7	41.1	19.6	8.8
1-15 Aug.	45.6	14.2	8.6	42.9	15.8	6.9	42.1	20.6	10.4
16-31 Aug.	47.5	13.4	8.9	44.9	14.1	7.5	43.7	19.6	11.0
1-15 Sept.	44.6	10.4	—	42.3	14.4	—	36.8	25.6	—
16-30 Sept.	45.2	13.8	8.7	47.3	15.0	—	40.3	21.8	8.7
1-15 Oct.	—	16.0	—	—	—	—	42.3	20.0	8.4

Fish with three rings were not clearly differentiated as a distinct age-group. Because of small numbers neither modes nor general shapes of the distributions could be clearly determined. Means tended to increase slightly as the season progressed. There was considerable overlap of the lower end of the length range with the upper end of the length range of two-ring fish.

If the rings we observed were true annuli, the distance from the last ring to the scale edge should have decreased as the number of rings increased, and should have increased throughout the season for fish having the same number of rings. Both of these trends were apparent (Table 6).

Mean lengths back-calculated to the age of annulus formation from fish with one, two, or three rings were similar, and the mean lengths at the time of first ring formation calculated from two-ring fish were slightly smaller than those calculated from one-ring fish, as would be expected (Table 7). This tendency for mean lengths back-calculated from successively older ages of the same year class to become progressively smaller is commonly known as Lee's phenomenon and may be caused by a variety of factors. Mean lengths calculated from three-ring fish, however, were slightly larger, rather than smaller, than mean lengths calculated from either one- or two-ring fish.

Frequency distributions of lengths back-calculated to the time of the first, second, and third ring formation were well separated from each other, with only a small overlap between one- and two-ring and two- and three-ring fish (Figure 2). Those at the time of the first ring formation were similar in shape, whether calculated from one-ring, two-ring, or three-ring fish. Those calculated from two-ring fish were shifted slightly farther to the left than those calculated from one-ring fish, as

TABLE 7.—Mean lengths (millimeters) of Gulf menhaden at the time of each ring formation calculated from one-, two-, and three-ring fish, 1968-72 year classes.

Year class	First ring			Second ring		Third ring
	1-ring fish	2-ring fish	3-ring fish	2-ring fish	3-ring fish	3-ring fish
1968	—	—	88.4	—	157.4	186.4
1969	—	95.2	96.6	164.5	166.1	195.1
1970	90.3	85.1	92.9	165.0	166.3	195.3
1971	95.0	86.3	—	158.9	—	—
1972	100.3	—	—	—	—	—

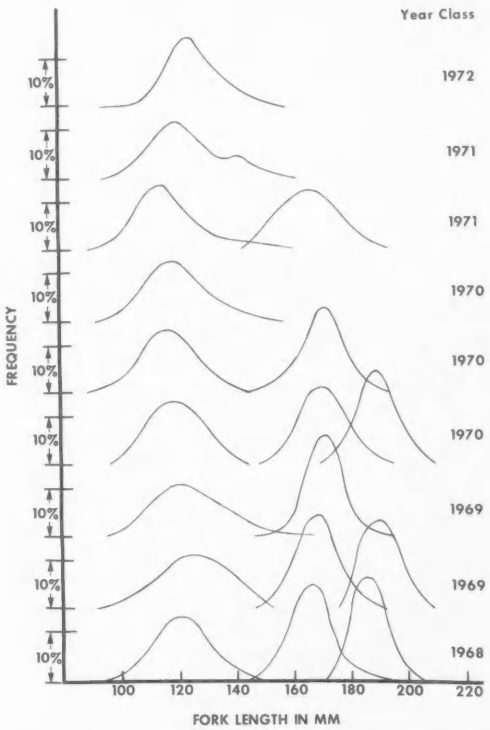

FIGURE 2.—Length-frequency distributions at time of first, second, and third ring formation, back-calculated from one-ring, two-ring, and three-ring Gulf menhaden, 1968-72 year classes.

would be expected. Those at the time of the second ring formation, whether calculated from fish with only a ring in the second position or from fish with both rings, were nearly identical and were shifted slightly to the right of distributions calculated from fish with three rings.

CONCLUSIONS

On scales of most Gulf menhaden with one or two rings, the rings appear to be true annuli. A relatively large number of fish that do not form a ring at the end of the first year form a ring at the end of the second year. A very small number that form a ring at the end of the first year do not form a ring at the end of the second year. It is possible, therefore, to separate age-2 from age-1 fish by the number of rings, or the location of the ring if only one is visible.

For fish having scales with more than two rings, or with two rings that are oddly spaced, it is difficult to differentiate between true and false annuli, or to determine to what year a particular ring should be assigned. On scales of some fish that could be age 3 on the basis of length, only two rings are visible, in what appears to be either the first and second or second and third positions. On some scales that have three well-defined rings, the spacing appears too unusual to be true annuli. For those fish that are called age 3, the lengths overlap those of age-2 fish, the mean lengths and ranges progress very little during the season, and the mean increments from the last annulus to the scale edge show little increase. We concluded that it is impossible to separate age-3 from age-2 fish with a high degree of certainty on the basis of the number or the location of scale rings.

From late August until October a small number of fish ranging from about 115 to 135 mm appear. We believe most of these fish, which have no scale rings, are age 0, but we cannot be certain because many of the fish in this size range of age-1 fish also have no scale rings.

The small number of tags recovered after 2 yr from fish tagged as juveniles, or age 0, the scarcity in the catch of fish larger than those with two rings, and the small numbers of fish with more than two rings, indicate that few Gulf menhaden live to be older than age 2. Since both age-0 and age-3 fish compose <2% of the catch, and since each age-group is either impossible or difficult to identify, we believe it is practical to recognize only two age-groups of Gulf menhaden: those age 1 or younger and those age 2 or older.

If only two ages are recognized, fish with no annuli can be aged by length. For each month, those below a certain fork length can be called age 1 or under, those above a certain length age 2 or older. Those in between cannot be individually aged, but the number in each length class can be apportioned to each age-group on the basis of the percentage of fish in each length class with one or two annuli. For example, in June 1971 (Table 3) all fish <165 mm may be called age 1, all >185 mm age 2. Of the 31 unaged fish 165-169 mm, 30 (97%) are age 1 and 1 (3%) is age 2; of the 45 between 170 and 174 mm, 37 (82%) are age 1 and 8 (18%) are age 2.

A question that may arise concerns the accuracy of previous aging methods. To shed some light on this question, we compared the percentages of fish at each age for methods 1 and 2. In method 1, fish ages had been based on a combination of factors: the general appearance of the scales, the number and location of rings, the fish length, and the time of year the fish was caught. In method 2, fish that had been aged by the number and location of scale rings, and fish that could not be aged, were grouped in 5-mm size classes. For each size class the number of unaged fish were apportioned to each age-group by the same percentage as fish that had been aged. We retained the age-3 group for comparative purposes, but could not differentiate between age-0 and age-1 fish.

The percentages at each age were remarkably similar, the differences between methods varying from only 0.1 to 2.7%. We concluded, therefore, that age compositions based on the previous method of aging are reliable and that valid inferences pertaining to population dynamics of Gulf menhaden can be based on them.

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VARIABILITY IN ZOOPLANKTON BIOMASS DISTRIBUTION IN THE NORTHERN SARGASSO SEA: THE CONTRIBUTION OF GULF STREAM COLD CORE RINGS[1]

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ABSTRACT

The scale and frequency of physical variability resulting from incursion of Gulf Stream cold core rings into the northern Sargasso Sea makes this faunal province more heterogeneous than previously recognized. At any one time such rings may cover between 6 and 13% of the surface area of the northern Sargasso Sea. They are more productive than the surrounding Sargasso Sea and have a zooplankton biomass intermediate between the Sargasso Sea and the slope water. Cold core rings may augment by 3 to 7% the primary productivity and by 8 to 16% the zooplankton standing crop of the northern Sargasso Sea. Compared with either the surrounding Sargasso Sea or their parent slope water, an unusually large percentage of the 0-800 m biomass in rings is found at depths greater than 200 m. This distribution may be related to hydrographic and biological changes associated with ring decay. Because of their higher productivity, differences in vertical biomass structure, and the possibility that ring food chain efficiency is lower than that of the Sargasso Sea, rings may provide a disproportionately large fraction of the total supply of organic matter to the northern Sargasso deep Sea.

A number of papers have characterized the zooplankton biomass of the northern Sargasso Sea (Menzel and Ryther 1961; Grice and Hart 1962; Bé et al. 1971; Deevey 1971; Deevey and Brooks 1971; and others). Because of the variety of methods employed in both sampling and processing, the results of these studies are not readily comparable. In general, previous authors have portrayed the Sargasso Sea as a remarkably homogeneous faunal province. The scale and frequency of regional variability resulting from incursions of cold core rings into the Sargasso Sea have not been generally appreciated. Cold core rings are mesoscale hydrological features 150 to 300 km in diameter and up to several thousand meters in depth. They form when southerly directed Gulf Stream meanders become so accentuated as to separate from the Stream and move south, enclosing a core of cold and relatively fresh slope water within a remnant of the Gulf Stream (Parker 1971; Fuglister 1972; Richardson 1976). It is likely that in the northern Sargasso Sea, at any one time, there are 10 to 15 such rings (Lai and Richardson 1977). Estimating the surface area of the northern Sargasso Sea as 32.9×10^5 km^2 (Jahn 1976), cold core rings may cover between 6 and 13% of this surface. (Throughout the ensuing sections, unless otherwise indicated, the terms ring, slope water, and Sargasso Sea denote hydrographic, not geographic, entities.)

An overview of the phytoplankton, zooplankton, and midwater fish populations inhabiting cold core rings has been given by Wiebe, Hulburt, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox (1976). The results of that study indicated that mean zooplankton biomass in the upper 750-800 m of rings between 3 and 10 to 12 mo of age was consistently higher than that in the surrounding Sargasso Sea. In these preliminary data the fraction of biomass below 250-300 m in depth was particularly large while the near surface was more similar to the Sargasso Sea. We have now taken vertically stratified hauls in the same ring 3 mo apart. The data from these hauls confirm our initial interpretation.

The objective of this paper is twofold. First, we describe the zooplankton biomass distributions characteristic of the northern Sargasso Sea, of a cold core ring, and to a lesser extent of the slope water—the source of ring water. Second, we will attempt to relate the patterns observed to systematic variations in phytoplankton standing

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crop, primary productivity, and water temperature, and to explore the significance of ring biomass distribution.

METHODS

The major portion of the data to be presented in this paper was collected on RV *Chain* cruise 125 (August 1975) and on RV *Knorr* cruise 53 (November 1975). The ring sampled (designated Ring-D by the Naval Oceanographic Office), was formed in February 1975. It was, therefore, about 6 mo old when first sampled and 9 mo old when sampled again in November. In November the slope water was hydrographically complex. It is likely that some of our intended slope water tows (MOC 39 and MOC 40) may have been taken in the vicinity of a warm core ring (Saunders 1971). The upper 200 m of the water column at that station was warmer and more saline than is typical for the slope water. In addition, infrared satellite photographs clearly show the presence of this warm ring during the period of sampling. Other slope water stations may have been influenced by the passage of a warm core ring. In analyzing the data, MOC 39 and 40 are considered separately and designated warm core ring tows. Data corroborating specific points or conclusions have been drawn from collections made on RV *Atlantis* cruise 71, RV *Chain* cruise 111, and RV *Knorr* cruises 35 and 38 (Table 1).

Collections in Gulf Stream cold core rings, the northern Sargasso Sea, and slope water were made with three types of sampling gear: on the early cruises 1-m diameter ring nets or modified opening/closing 70-cm diameter bongo nets (McGowan and Brown 1966), on the two most recent cruises a multiple opening/closing net and environmental sensing system—MOCNESS (Wiebe, Burt, Boyd, and Morton 1976)—with a mouth area of 1 m × 1.4 m (effective area is 1 m²). All nets were constructed from 0.333-mm Nitex[3] gauze; depth recorders and flow meters were used on all tows.

The 1-m nets were hauled obliquely, ideally to a depth of 800 m. On some cruises a second haul was taken to a depth of 300 m. Bongo nets were towed obliquely within the depth intervals 0-250, 250-500, and 500-750 m. With occasional exceptions, the MOCNESS sampled both from 800 m to the surface in 100-m intervals, and from 200 m to the surface in 25-m intervals. Sampling with 1-m and bongo nets was almost always done at night, while at most MOCNESS stations samples were taken both day and night. The types of tows taken on the five cruises are given in Table 1. All samples were preserved in 5-10% Formalin buffered to pH 8.0 with sodium tetraborate. In the vicinity of all plankton hauls, hydrographic casts were made yielding nearly concomitant vertical profiles of temperature, salinity, oxygen, chlorophyll, nutrients, primary productivity, and phytoplankton species (see Wiebe, Hulburt, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox 1976 for methods).

Zooplankton biomass was measured by the method of Ahlstrom and Thrailkill (1963) after removal of all organisms greater than 5 cm³. Displacement volumes were measured 5 to 9 wk after a cruise. No attempt has been made in this paper to partition the biomass according to taxa. The species composition of those samples already examined appears similar to that reported for the region by Grice and Hart (1962), Deevey (1971), and Deevey and Brooks (1971).

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Summary of slope water, ring, and Sargasso Sea zooplankton sample stations.

Cruise	Date	Age of ring (mo)	Number of samples (stations)			Type of net
			Ring	Sargasso Sea	Slope water	
Atlantis II 71[1]	21 Sept.-14 Oct. 1972	10-12	8(4)	28(15)	4(2)	1 m
Chain 111[1]	7 Feb.-18 1973	3.5	6(2)	5(2)	2(2)	1 m and bongos
Knorr 35[1]	23 Nov.-3 Dec. 1973	3.0	8(4)	1(1)	5(3)	1 m and bongos
Knorr 38[1]	12 Feb.-3 Apr. 1974	10-12				1 m
Chain 125[2]	4 Aug.-17 1975	6.0	48(1)	32(2)	48(2)	MOCNESS
Knorr 53[3]	17 Nov.-1 Dec. 1975	9.0	48(1)	40(2)	64(3)	MOCNESS

[1]Positions of stations illustrated in Wiebe, Hulburt, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox (1976).
[2]Sargasso Sea: MOC 1,2 (35°37′, 68°31′), MOC 3,4 (35°22′, 68°17′), MOC 12 (34°11′, 71°40′), MOC 13,14,15 (34°10′, 71°34′); ring: MOC 5,11 (34°29′, 69°56′), MOC 6,7 (34°34′, 69°52′), MOC 8 (34°31′, 69°49′), MOC 10 (34°33′, 69°53′); slope water: MOC 16,17 (38°02′, 69°59′), MOC 18,19 (38°05′, 70°02′), MOC 20,21 (39°05′, 70°12′). All positions are north latitude and west longitude.
[3]Sargasso Sea: MOC 23,24,25 (32°44′, 71°10′), MOC 26 (32°52′, 71°08′), MOC 34 (34°12′, 70°30′); ring: MOC 27, 28, 29 (33°49′, 71°54′), MOC 31 (35°50′, 71°48′), MOC 32 (33°56′, 71°54′), MOC 33 (34°03′, 71°56′); warm core ring: MOC 39,40 (40°04′, 68°05′); slope water: MOC 35,36 (38°51′, 67°47′), MOC 37,38 (38°55′, 67°46′), MOC 41,42 (39°59′, 69°00′). All positions are north latitude and west longitude.

RESULTS

Regional Biomass

The biomass collections obtained in the same ring 3 mo apart in August and November 1975 corroborate differences already noted in 0-800 m zooplankton biomass between the Sargasso Sea, cold core rings, and slope water (Figures 1, 2). In both months the slope water 0-800 m biomass was larger than either the Sargasso Sea or ring 0-800 m biomass (Mann-Whitney U-test, $P<0.01$). In August, the contrast between slope water and the two other regions was particularly marked with average concentration in the upper 800 m approximately 10-12 times larger than in the Sargasso Sea and ring (Table 2, top). At several depths in the August slope water stations the zooplankton biomass was dominated by *Salpa aspera*.[4] Differences in abundance of this salp accounted for a large part of the variation between slope water stations. The high water content of these animals undoubtedly caused our estimate of biomass by displacement volume to be considerably higher than had we measured dry weight or organic carbon content. It is clear, nonetheless, that the standing stock of zooplankton was exceedingly large.

Relative to the Sargasso Sea, 0-800 m ring biomass was on the average 1.36 times larger in August and 1.33 times larger in November (Table 2, bottom). These differences are consistent with data from previous cruises; using paired regional biomass averages observed on all cruises to date (Table 3) we see that the mean zooplankton biomass in rings and in the Sargasso Sea is significantly different (Sign test, $P<0.05$).

In November zooplankton standing crop was consistently lower than in August with the most pronounced change occurring in the slope water. Although *S. aspera* was still present at the slope water stations, it no longer dominated the biomass. Comparing August and November 0-800 m biomass averages, segregating day and night samples for each region, we see that the overall seasonal decline is statistically significant (Sign test, $P<0.05$, computed using cubic centimeters per square meter in Figures 1 and 2). Indeed only one November 0-800 m biomass value was as large as the smallest 0-800 m biomass in the same region in August.

TABLE 2.—Comparison of slope water, ring, and Sargasso Sea zooplankton biomass (cm^3/m^2) based on weighted averages of day and night samples collected at 0-800, 200-800, and 0-200 m depth intervals. Number of tows used to make average given in parenthesis.

	August 1975			November 1975		
Region	0-800	200-800	0-200	0-800	200-800	0-200
Sargasso Sea	16.6(4)	8.8(4)	8.1(8)	10.2(2)	5.6(2)	6.0(4)
Ring fringe				9.1(1)	4.3(1)	4.8(1)
Cold core ring	22.5(3)	15.6(3)	6.4(6)	13.6(4)	11.4(4)	3.4(5)
Slope water	256.2(4)	95.6(4)	121.8(6)	33.8(4)	23.0(4)	12.8(6)
Warm core ring				27.9(2)	17.2(2)	10.8(2)

	Ratio ring/Sargasso Sea		
Month	0-800	200-800	0-200
August	1.36	1.77	0.79
November	1.33	2.03	0.56

In November 0-800 m ring biomass was on the average 0.79 times smaller than in the Sargasso Sea, while in August it was 1.36 times larger. Comparing August and November 0-800 m ring biomass averages, segregating day and night samples for each region, we see that the overall seasonal decline is statistically significant (Sign test, $P<0.05$, computed using cubic centimeters per square meter in Figures 1 and 2). Indeed only one November 0-800 m ring biomass value was as large as the smallest 0-800 m ring biomass in August.

[4]The significant biomass contribution of *S. aspera* is discussed in Wiebe, P. H., L. P. Madin, G. R. Harbison, L. R. Haury, and L. M. Philbin. 1977. Diel vertical migration by *Salpa aspera* and its potential for large-scale particulate organic matter transport to the deep-sea. Submitted to Mar. Biol.

TABLE 3.—Average zooplankton biomass in slope water, ring, and Sargasso Sea—dry weight (mg/m^3) in column ≈750 m deep. Numbers of stations per area and range of biomass values (after colon) given in parenthesis. This table is an expanded version of table 3 in Wiebe, Hulburt, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox (1976). Note that the biomass units in the original table were incorrectly presented as milligrams per square meter.

Cruise	Slope water		Ring		Sargasso Sea		Ring age (mo)	Ring ÷ Sargasso	Slope ÷ Sargasso
Atlantis II 71	7.43	(1)	2.24	(4:2.06-2.60)	1.68	(4:1.34-2.05)	10-12	1.33	4.42
Chain 111	4.21	(1)	4.95	([1]2:2.21-7.68)	2.70	([2]3:1.99-3.96)	3.5	1.83	1.56
Knorr 35	6.06	([3]4:3.60-7.74)	3.67	([4]3:3.15-4.33)	2.47	(1)	3.0	1.49	2.45
Knorr 38[5]	5.74	(4:2.2-9.14)	3.10	(6:2.56-4.98)	2.34	(4:1.76-3.21)	10-12	1.32	2.45
Chain 125[5]	9.10	([6]2:6.85-11.35)	2.26	(3:1.73-2.57)	1.49	(4:0.90-1.97)	6	1.52	6.11
Knorr 53[5]	3.43	(4:2.77-4.03)	1.09	(4:0.72-1.35)	0.83	(2:0.80-0.86)	9	1.31	4.13
Mean							7.3	1.47	3.52

[1]Each of the two values is integrated for the water column based on three stratified bongo net tows.
[2]Two values are from oblique meter net tows; one is an integrated value based on three stratified bongo net tows.
[3]Two values are from oblique meter net tows; one is an integrated value based on three bongo net tows; one is an oblique bongo net tow.
[4]One value is an integrated value based on three stratified bongo net tows; two values based on two stratified bongo net tows.
[5]Cubic centimeters per cubic meter converted to milligrams per cubic meter using equation 4 table 2 in Wiebe et al. (1975). Note that this conversion affects the regional biomas ratios (see Figure 2) because the relationship between displacement volume and dry weight is not linear.
[6]Salp-rich tows, MOC 39 and MOC 40, excluded.

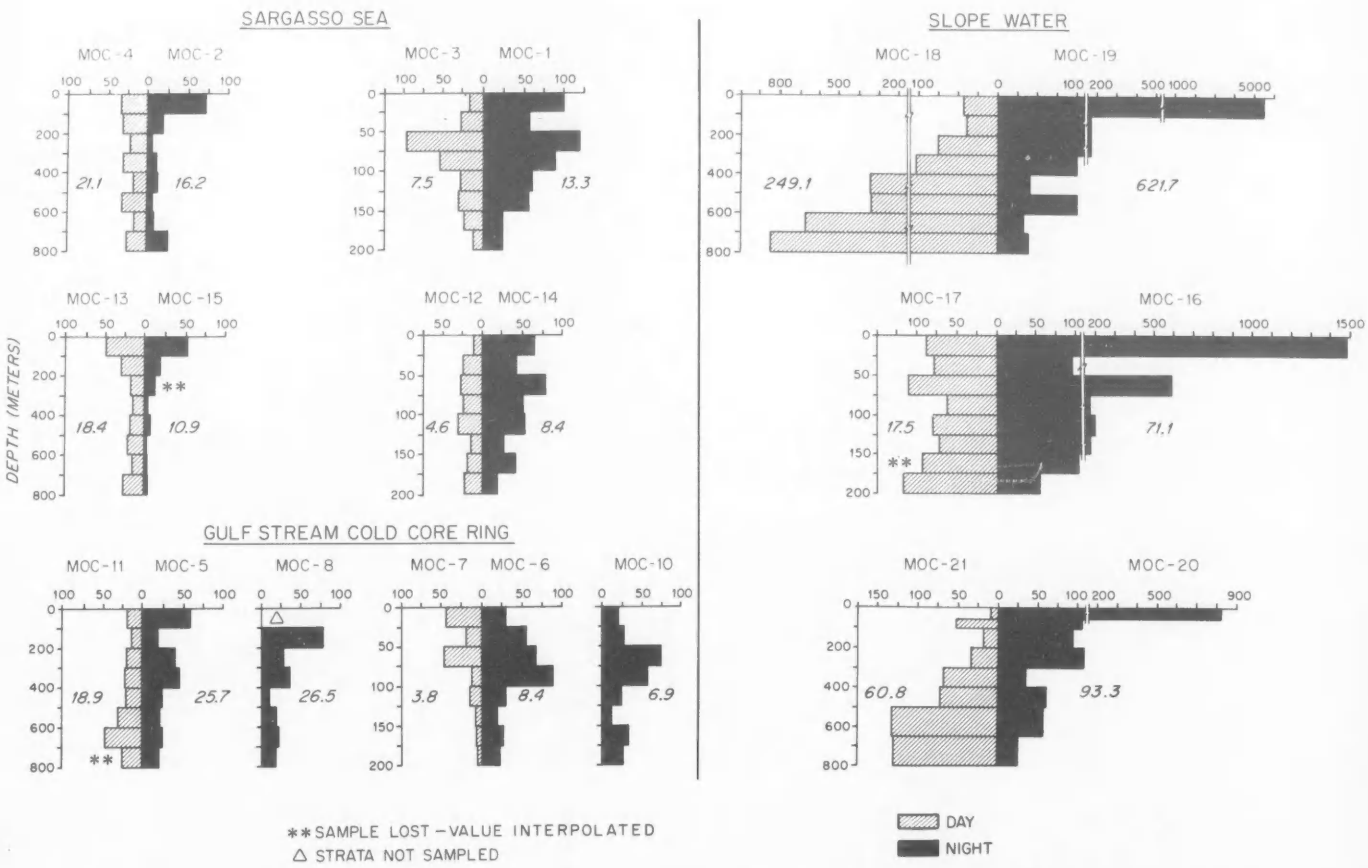

FIGURE 1.—Slope water, ring, and Sargasso Sea zooplankton biomass ($cm^3/1{,}000\ m^3$). August 1975—*Chain* cruise 125. Values associated with each profile are cubic centimeters per square meter for the entire portion of the water column sampled. Note that 0-200 m profiles have an expanded vertical depth scale.

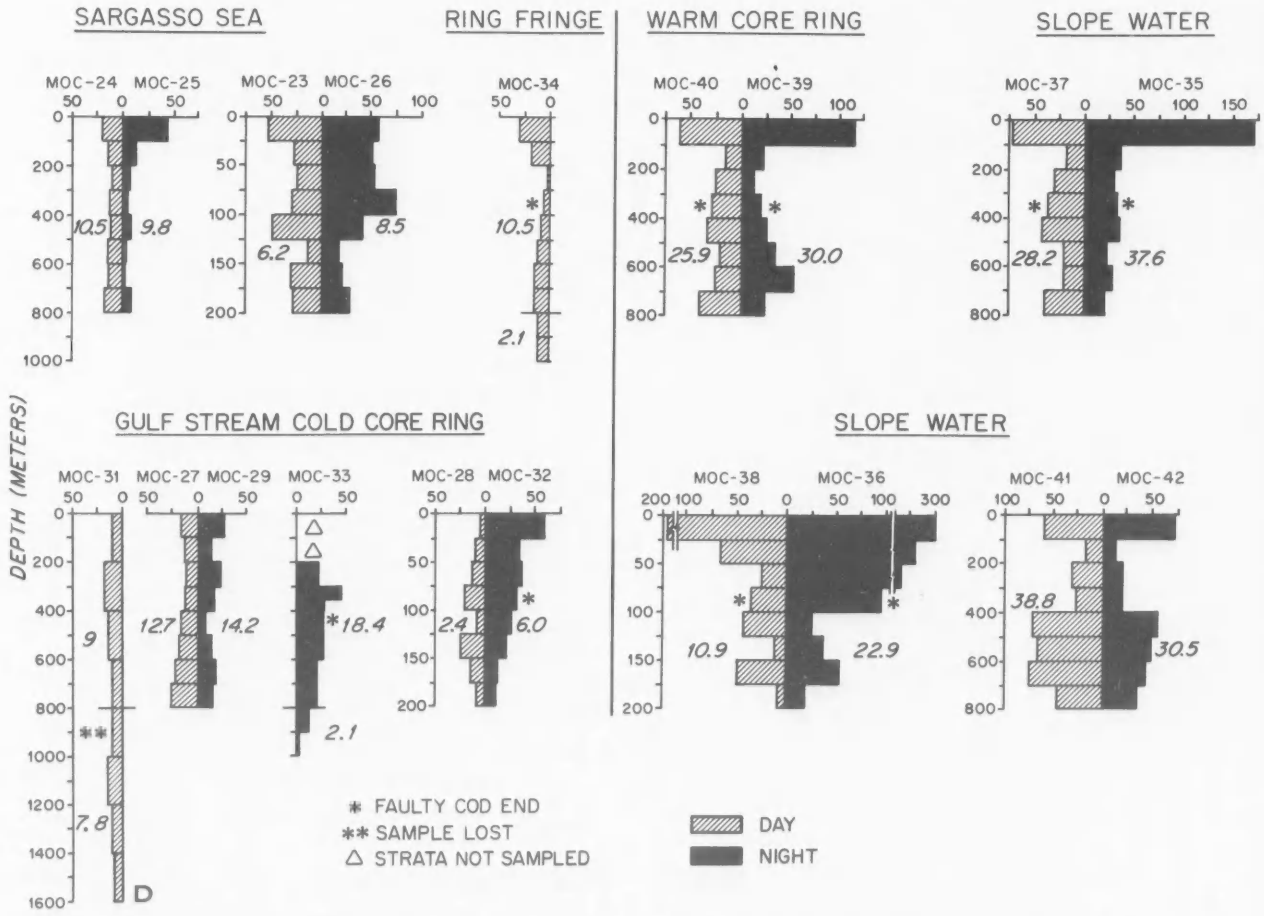

FIGURE 2.—Slope water, ring, and Sargasso Sea zooplankton biomass ($cm^3/1{,}000\ m^3$). November 1975—*Knorr* cruise 53. Values associated with each profile are cubic centimeters per square meter for the water column sampled except for MOC-31, MOC-33, and MOC-34, where values have been calculated for above and below 800 m. Note that 0-200 m profiles have an expanded vertical depth scale.

Average Vertical Structure

Comparing Ring-D biomass partitioned according to depth, the upper 200 m in the ring contained, on the average, less biomass during both sampling periods than did the Sargasso Sea (Table 2, top). This was true both day and night during the August and November cruises. In contrast, ring biomass between 200 and 800 m was higher both day and night (Figures 1, 2). The range of 200-800 m biomass values in the ring and in the Sargasso Sea does not even overlap. The combination of lower average surface biomass and higher average subsurface biomass in the ring is highly significant (Sign test, $P<0.01$, computed using sums of 0-200 m and 200-800 m $cm^3/1{,}000\ m^3$ derived from Figures 1 and 2). The regional weighted averages of percent 0-800 m biomass present in the upper 200 m in August were 51%, 34%, and 27% in the Sargasso Sea, slope water, and ring, respectively. In November these averages were 45%, 32%, and 25% (Table 4). Although very different sampling systems and tow strategies were employed, data from *Atlantis II* cruise 71 corroborate the direction of difference of these observations in that the percentages of 0-800 m biomass found at night in the upper 300 m were 64% and 52% for the Sargasso Sea and ring, respectively (Table 5). In addition, the 300-800 m biomass was 1.73 times larger in this latter ring than in the surrounding Sargasso Sea.

TABLE 5.—Ring and Sargasso Sea zooplankton biomass—*Atlantis II* cruise 71 (mg/m^2).

Area	0-300 m	0-800 m	$\frac{0\text{-}300}{0\text{-}800} \times 100$	
Ring	954	1,648	58%	52%
	963	2,080	46%	
	930	1,704	55%	
	828	1,728	48%	
Sargasso Sea	858	1,344	64%	64%
	798	1,072	74%	
	765	1,640	47%	
	921	1,304	71%	

Diel Migration

Complicating these general observations and contributing to sample variability are day/night differences in biomass distributions (Table 4). In all day/night sample pairs the fraction of 0-800 m biomass present in the 0-200 m interval is larger in the night sample (Sign test, $P<0.01$). This results from either diel migration or day/night differences in avoidance within the comparatively well-illuminated surface layers. Avoidance does not appear to be an important factor because at some stations the day 0-800 m biomass exceeds the night 0-800 m biomass. This is true in all Sargasso Sea 0-800 m sample pairs and at one slope water station (Figures 1, 2). Furthermore, some species of zooplankton taxa already enumerated, e.g., euphausiids and pteropods, exhibit strong diel migration patterns in all three areas.

Since we believe diel migration to be the appropriate explanation, the data further suggest that while essentially the same percentage of 0-800 m biomass was migrating into the surface layers of the Sargasso Sea (24-30% during both sampling periods), there was a reduced percentage migrating in the ring in November (21% in August versus 9% in November—Table 4). Although a smaller proportion of the biomass may have been migrating in the ring relative to the Sargasso Sea, there was a significantly greater (Mann-Whitney U-test, $P<0.05$) day/night biomass ratio in the

TABLE 4.—Percent of 0-800 m slope water, ring, and Sargasso Sea zooplankton biomass in the upper 200 m (800 m tows only). D = Day; N = Night.

	August 1975					November 1975				
Region	Percentages of individual tows	D	N	N−D	(D + N)/2	Percentages of individual tows	D	N	N−D	(D + N)/2
Sargasso Sea	$D_1 = 32$	39	63	24	51	$D_1 = 30$	30	60	30	45
	$N_1 = 57$					$N_1 = 60$				
	$D_2 = 41$									
	$N_2 = 69$									
Ring fringe						$D_1 = 46$	46			
Cold core ring	$D_1 = 16$	16	37	21	27	$N_1 = 29$	20	29	9	25
	$N_1 = 32$					$D_1 = 21$				
	$N_2 = 42$					$D_2 = 19$				
Slope water	[1]$D_1 = 3$	7	61	54	34	$D_1 = 32$	23	41	18	32
	[1]$N_1 = 93$					$N_1 = 55$				
	$D_2 = 7$					$D_2 = 13$				
	$N_2 = 61$					$N_2 = 27$				
Warm core ring						$D_1 = 30$	30	46	16	38
						$N_1 = 46$				

[1]On this tow series, MOC 18 and 19, salps were extremely dominant. These tows are excluded from averages.

upper 200 m in the ring (Table 6). This apparent contradiction results from the fact, already noted, that the percentage of 0-800 m biomass present in the upper 0-200 m was very much greater in the Sargasso Sea. Day/night ratio of biomass in the upper water column is often used to measure intensity of diel migration; clearly the meaning of this ratio is highly dependent upon average vertical biomass distribution.

Slope water day/night sample pairs may be interpreted as documenting diel migration, but the data are extremely variable both within and between cruises (Table 4). There may have been a less well-developed migration in the fall, but the generality of this is questionable.

TABLE 6.—Day/night differences in slope water, ring, and Sargasso Sea zooplankton biomass in the upper 200 m.

Region	Ratio night/day			
	August 1975		November 1975	
Sargasso Sea	[1]1.78	[2]1.37	[1]1.37	[2]1.86
	[1]1.84	[2]0.99		
Cold core ring	[1]2.01	[2]3.10	[1]2.48	[2]1.86
Slope water	[1]4.06	[2,3]68.33	[1]2.10	[2]2.27
		[2,3]14.82		[2]1.70

[1]Based on 0-200 m tows.
[2]Based on 0-800 m tows.
[3]Ratio affected by extreme salp dominance.

Shallow Biomass Structure

In the 0-200 m biomass profiles, an intermediate biomass peak occurred between 50 and 100 m depth at nearly every station in August 1975 (Figure 1: MOC 1, 3, 6, 7, 10, 16, 17). At all but one of the Sargasso Sea and ring stations this intermediate peak is the highest observed value in the 0-200 m tows. At slope water stations of the same cruise this intermediate peak is the second highest observed value. If we rank each interval in a profile in order of zooplankton abundance, we can test the significance of this observation. For instance, the individual summer tows in the ring and the Sargasso Sea exhibit significant concordance as to which depth intervals have the larger and which the smaller zooplankton biomass (Friedman 2-way analysis of variance on ranks, $P<0.005$). Given this result, the best estimate of the differences between intervals is the order of their summed ranks (i.e., 50-75 m>75-100 m>100-125 m>25-50 m>0-25 m>150-175 m>125-150 m>175-200 m). Applying a procedure for testing differences between individual depth intervals (Nemenyi 1963), we see that concordance results from the fact that the 50-75 m biomass is significantly greater than the biomass in the intervals 125-150, 150-175, and 175-200 m, and the 75-100 m biomass is greater than the 175-200 m biomass ($P<0.05$). An intermediate peak is not a notable feature of any of the 0-200 m profiles taken on the fall cruise with the exception of the Sargasso Sea sample pair (Figure 2: MOC 23, 26).

DISCUSSION

Wiebe, Hulburt, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox (1976) have discussed the formation and decay of an idealized cold core ring. Initially conditions inside a ring core are identical to those in the slope water just northward of the Gulf Stream at the time of ring formation. Through time the ring decays; the isotherms deepen, the water becomes more saline, the O_2 minimum deepens, and the constituent flora and fauna either die off or become diluted by populations from the surrounding Sargasso Sea. Because zooplankton populations are generally suited to the environmental conditions they encounter within their normal range, this decay process may be viewed as the gradual imposition of a complex environmental stress upon an entire community. Wiebe, Hulbert, Carpenter, Jahn, Knapp, Boyd, Ortner, and Cox (1976) have documented some of the intermediate stages in this idealized process. In fact, this process can be aborted when a ring is reabsorbed by the Gulf Stream (Fuglister 1972; Richardson et al. 1977). All biological and physical properties are not equally conservative so their decay rates would not be the same.

Regional Contribution of Cold Core Rings

PRIMARY PRODUCTIVITY.—It is well known that slope water is more productive than the Sargasso Sea. Ryther (1963) estimated that slope water is about twice as productive on an annual basis (120 g C/m² per yr versus 60 g C/m² per yr). Although our own data are scanty, rings on the average are intermediate between slope water and the Sargasso Sea (Table 7). A few simplifying assumptions permit budgetary computations to be made regarding the overall effect of rings on the carbon budget of the northern Sargasso Sea. Let us assume an average ring life of 1 yr and a linear rate of decay of productivity (i.e., that annual ring production is the arithmetic mean of annual Sargasso Sea and slope water production). Allowing 6 to 13% as the areal contribu-

TABLE 7.—Summary of slope water, ring, and Sargasso Sea primary productivity (mg C/m² per day), phytoplankton carbon[1] (mg/m²), and chlorophyll *a* (mg/m²) measurements.

Region	March 1974		August 1975		Phytoplankton carbon	November 1975		Phytoplankton carbon
	Productivity	Chlorophyll	Productivity	Chlorophyll		Productivity	Chlorophyll	
Sargasso Sea	228.5	46.4	[2]207	13.3	33.4	86.5	12.0	21
			100			252.2		
Cold core ring	440.1					483.2		
		73.0	83	17.3	45			28.2
	333.1		106			155.5	10.3	
						186.5		
Slope water	1,025.5		175			1,302.2		
		70.4		50.5				
	368.4		270		280	824.0	39	287
						376.2		
						363.7		

[1]Based on counts of cells larger than 4-5 μm.
[2]The high value in average mg C/m² per day observed at this station is a consequence of one unusually high surface value.

tion of rings to the northern Sargasso Sea as explained earlier, and Ryther's estimate of a twofold difference in annual production, the net annual production of the geographic northern Sargasso Sea is then 3 to 7% higher than if it contained no rings (i.e., $6 \times 1.5 = 9$, $9 + 94 = 103$ and $13 \times 1.5 = 20$, $20 + 87 = 107$). Our assumption of linear decay is most certainly an oversimplification. In November 1975, the ring water column, like the slope water, began its winter overturn before the surrounding Sargasso Sea. Mixing eroded the seasonal thermocline that had been observed in Ring-D in August 1975. The decay we have assumed was reversed, and ring productivity was enhanced (Table 7).

ZOOPLANKTON STANDING CROP.—Similar calculations can be made regarding the relative contribution of rings to the mean zooplankton biomass of the geographic northern Sargasso Sea. Neglecting one station which had anomalously high values due to extreme salp dominance, the average of slope water biomass values is 3.5 times the observed Sargasso Sea biomass (Table 3). Given this ratio and the same linear [i.e., $(3.5 + 1) \div 2 = 2.25$] and areal assumptions made earlier, rings may augment the zooplankton standing crop of the geographic northern Sargasso Sea by 8 to 16% (i.e., $6 \times 2.25 = 14$, $14 + 94 = 108$ and $13 \times 2.25 = 29$, $29 + 87 = 116$). Our ratio of slope water to Sargasso Sea biomass may be compared with that of Grice and Hart (1962), who reported the slope water standing crop as three to four times that of the Sargasso Sea. They also excluded extremely salp-rich samples in making this comparison. Our assumption of 2.25 as an annual mean ring/Sargasso biomass ratio (i.e., linear decay) may be an overestimate considering the average biomass ratio obtained on all cruises to date and the average ring age sampled (Table 3). On the other hand some rings do last longer than a year and the lowest ring:Sargasso Sea ratios that we have observed are approximately 1.3 (i.e., >1.0).

We have noted a highly significant decline in 0-800 m biomass from August to November in slope water, ring, and Sargasso Sea both in data presented here and in data more recently collected.[5] This observation is consistent with those of Grice and Hart (1962) with respect to the slope water. They noted, however, no such decline in the Sargasso Sea. Neither is there a summer-to-fall decline in the Sargasso Sea data of Deevey (1971). The Sargasso Sea and slope water data of Fish (1954) exhibit irregular fluctuations in biomass throughout the summer and fall. Moore (1949) presented some Sargasso Sea data indicating a progressive decline of biomass from a spring maximum to a fall minimum. Their data substantiate that interseasonal fluctuations in the Sargasso Sea are less marked than in the slope water.

Vertical Structure

We have pointed out that, compared with either the Sargasso Sea or slope water, an unusually small percentage of 0-800 m biomass is present in the upper 200 m of a ring. We found a relatively large fraction of the 0-800 m zooplankton biomass above 200 m in the northern Sargasso Sea. The netting employed by Leavitt (1935, 1938) was relatively coarse (1.0 mm) so it is difficult to compare our results with his. Nonetheless, at his two Sargasso Sea stations (2462, 2463) the percentages of

[5]Some of this data is presented in figure 4 of Richardson, P. L., J. Schmitz, and P. H. Wiebe. 1977. Gulf Stream ring experiment. Polymode News 25:3. Unpubl. manuscr.

0-800 m biomass present in the upper 200 m were 42 and 49% which corresponds closely to our values (Table 3). Both of our results are virtually identical with those obtained by Menzel and Ryther (1961). From their table 1 we can calculate the percentages of 0-500 m biomass and 0-1,000 m biomass present above 200 m. Averaging the results, we find 44% of the 750-m biomass was present during the day above 200 m. Iashnov (1961) presented data for the Sargasso Sea in which 90% of the 0-1,000 m plankton was present above 200 m, but he used a relatively fine mesh net (0.180 mm). Unfortunately, Deevey and Brooks (1971) characterized 500-m depth intervals with horizontal tows at the midpoint of each interval to 2,000 m, while Grice and Hart (1962) sampled only the upper 100-200 m.

Several authors suggest that a vertical biomass structure similar to our slope water and Sargasso Sea observations is to be expected in temperate or subtropical oceanic environments relatively free of advective inputs. Vinogradov (1968: figure 47 and stations 3206 and 3829 in table 18) gave examples of oceanic regions with such a distribution. Zenkevich and Birstein (1956) agreed that zooplankton biomass in the North Pacific rather steadily decreases from the surface downwards, although the most marked reduction they discuss might be below our lowest standard sampling depth. The one very deep tow series we obtained in a ring, however, gave no indication of such a reduction (Figure 2, MOC 31).

Zooplankton biomass profiles obtained by Murano et al. (1976) in the northwest Pacific above the Sagami Trough exhibit the expected decrease with depth. Reanalyzed in our manner, the data of Marlowe and Miller (1975) for Station P in the North Pacific support the above generalization; the percentage of their 0-500 m biomass found at night in the upper 200 m was 57%. If one extrapolates their 500-m values as approximately applicable to the 500-800 m interval—a conservative approach for this argument—the resulting percentage becomes 49% (N). This is not unlike our average slope water percentage of 51% (N) and quite distinct from the average ring percentage of 33% (N) (Table 4). Station P is very different from Ring-D in respect to its vertical biomass distribution.

In slope water, the intermediate biomass peak in the upper 200 m approximately coincides with the depth of a nitrite maximum of the type discussed by Vaccaro and Ryther (1960). Our results and those of Marlowe and Miller (1975) appear to differ: they felt that the shallow nitrite peak of Station P was avoided by zooplankton. Since the levels of nitrite we have observed at the maximum are only slightly lower than those reported by Marlowe and Miller (0.2-0.5 μg A-N-NO_2/l versus 0.64 μg A-N-NO_2/l), our findings cast doubt on their speculation that nitrite toxicity might have been involved in the maintenance of the biomass minima they observed.

Explanations for Ring Biomass Structure

Given the relatively high zooplankton biomass of the slope water, it is clear why cold core rings have a higher average zooplankton biomass than the Sargasso Sea. Further, their higher average primary productivity appears responsible for this differential persisting 10-12 mo after ring formation. Our data suggest the decline in ring biomass takes place rather slowly; the oldest rings sampled (10-12 mo) had ring/Sargasso biomass ratios only 20% smaller than the same ratios in the newest rings sampled (3.0 and 3.5 mo, Table 3). Although physically and chemically intermediate between slope water and Sargasso Sea, rings appear to be unique in their vertical distribution of biomass.

We offer two logically distinct explanations for the small fraction of the 0-800 m biomass found within the upper 200 m of a ring. They are not mutually exclusive and the relative importance of these explanations is species dependent. The simpler argument stresses the importance of a physical factor—temperature. If a slope water animal were physiologically restricted to a particular temperature range, its habitat would descend as the ring decayed and isotherms sank. To the extent that the zooplankton population in the slope water exhibited this behavior, ring biomass distributions would deepen. This could apply only to a species which in its home range—the slope water—remains beneath the seasonal thermocline (i.e., moderately deep-living and exhibiting limited diel migration). Such a species would most likely have to be either carnivorous or omnivorous. Wiebe and Boyd (1978) have documented such a phenomenon for the slope water euphausid species, *Nematoscelis megalops*.

A more complex explanation stresses the importance of a biological factor—food resources. The kinds of changes that accompany ring decay must have a substantial effect upon zooplankton-phytoplankton interactions. Using unpublished

data obtained in August 1975 from 5 nine bottle hydrocasts, the number of phytoplankton cells per liter averaged 10,000 in the slope water, 2,500 in the ring, and 2,000 in the Sargasso Sea. Cells smaller than 4-5 μm were not enumerated and were, therefore, excluded from these computations. Values were integrated from 0 to 200 m—a conservative procedure tending to reduce slope water versus ring or Sargasso Sea differences. The species composition of the ring, while distinct, was more like that of the Sargasso Sea than that of the slope water. Again, considering the 0-200 m depth interval, the number of different phytoplankton species an animal would have encountered in a liter of water would, on the average, have been 6.0 (slope water), 9.6 (ring), and 10.4 (Sargasso Sea). Converting the mean cell volume of each species to carbon (Strathmann 1967) and multiplying by the number of individuals present, yielded values of average phytoplankton carbon of 1,400, 200, and 140 ng C/l. Thus, to acquire the same ration of food, a herbivore would have had to filter more than five times more water in the ring than in the slope water, and even more in the Sargasso Sea. In addition, the evenness of species' carbon equivalence was 0.46, 0.75, and 0.76. That is, the total carbon per liter was more evenly distributed among different species in the ring and the Sargasso Sea than in the slope water. (Evenness equals H/H_{max} (Pielou 1966) where H is the Shannon-Weaver diversity index computed upon species carbon equivalence rather than abundance and $H_{max} = \log_e S$ where S = number of species.) This last result implies that a herbivore capable of selecting by carbon content (i.e., particle size) would have found it less advantageous to concentrate on a particular species in the Sargasso Sea and the ring than in the slope water.

These properties of the phytoplankton population, i.e., species composition, carbon concentration, cell concentration, and cell carbon distribution, have profound effects on a filter-feeding herbivore's harvesting ability. We believe that early in ring evolution herbivorous slope water species are deleteriously affected and, therefore, may be replaced by Sargasso Sea forms more quickly than deeper living carnivorous or omnivorous slope water species. If we are correct, ring biomass distribution may deepen in part because a ring's 0-200 m biomass declines more rapidly than does its 200-800 m biomass.

Identification of some of the taxa in August 1975 samples, although limited, support the argument that in Ring-D epizooplanktonic herbivores were replaced before epizooplanktonic carnivores or omnivores. The species list of Ring-D thecosomatous pteropods, a largely herbivorous group, was quite similar to that of the surrounding Sargasso Sea.[6] Grice and Hart (1962) found that chaetognaths, a purely carnivorous group, were considerably more abundant in the Sargasso Sea than they are in slope water. In 6 nine-net fine-mesh tow series (12.5 cm diameter, Clarke-Bumpus nets with 67 μm mesh) taken in August, chaetognaths were five to ten times more abundant in the surrounding Sargasso Sea than they were in Ring-D. Other epizooplanktonic carnivores, e.g., *Stylocheiron suhmii* and *S. abbreviatum*, which are routinely found in the Sargasso Sea were not found in Ring-D August MOCNESS tows.

Organic Flux to Deep Sea

Rings may contribute a disproportionate fraction of the utilizable organic material available to the northern Sargasso deep sea. We feel this is likely both because of their generally higher productivity and because of their unique zooplankton biomass distribution and the factors that have resulted in that distribution. Ring zooplankton biomass below 200 m, in that it exceeds Sargasso Sea biomass and ultimately declines to a similar level, contributes to this augmentation. Differential seasonal mixing processes could also increase downward particulate flux. For example, in November 1975 we observed that winter mixing had proceeded further in Ring-D than in the surrounding Sargasso Sea water column. Herbivorous ring zooplankton (i.e., Sargasso forms) may have been unable to fully capitalize upon the sudden opportunity afforded by the increased primary production that accompanied the mixing (Table 7). If so, a larger fraction of this enhanced phytoplankton production would sink into the aphotic depths. Physical evidence obtained on two cruises undertaken to study rings during the summer has suggested to us that the seasonal thermocline may often be less stable in rings than in the Sargasso Sea.

Finally, there is a possibility of enhanced contribution of organic matter into the deep sea due to a lower overall trophic efficiency within the upper 200 m of rings (and slope water). If we divide

[6]John Wormuth, unpubl. data; cited with permission.

average 0-200 m zooplankton biomass (milligrams of carbon per square meter calculated using equation 4, table 2 in Wiebe et al. 1975) by 0-200 m phytoplankton carbon (milligrams of carbon per square meter from Table 5), excluding salp-rich MOC 18 and 19, we obtain the following ratios:

	Sargasso Sea	*Ring*	*Slope water*
Aug. 1975	253	138	84
Nov. 1975	332	131	28

Ratios in the ring are low, as are those in the slope water. Lower ratios suggest to us lower overall trophic efficiency within the upper 200 m. Although biased in that many cells are quite small, particularly in the Sargasso Sea, phytoplankton carbon of cells >5 μm is probably a reasonable estimate of the food available at the time of sampling to many of the herbivorous animals caught by our 0.333-mm mesh nets. The direction of difference noted above conforms with ideas expressed by Menzel and Ryther (1961), Heinrich (1962), and others who argued that especially close phytoplankton-zooplankton coupling may characterize oceanic tropical-subtropical waters.

The biomass data presented here illustrate the fact that geographic demarcation of oceanic faunal provinces is not sufficient. Hydrographic as well as faunal mapping is essential in explaining that portion of station-to-staion variability associated with mesoscale hydrographic variability resulting from phenomena like Gulf Stream cold core rings.

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RELATIVE CONTRIBUTION OF HUDSON, CHESAPEAKE, AND ROANOKE STRIPED BASS, *MORONE SAXATILIS*, STOCKS TO THE ATLANTIC COAST FISHERY

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ABSTRACT

Morphological characters were used in discriminant analysis to quantitatively estimate the relative contribution of striped bass, *Morone saxatilis*, stocks from various estuaries to the striped bass fishery along the Atlantic coast. Representative samples of the spawning stocks of the Hudson River, Chesapeake Bay system, and Roanoke River were collected and counts and measurements were taken on each specimen. Discriminant functions based on five morphological characters correctly classified approximately 75% of the specimens. The effectiveness of three types of estimates based on these functions in accurately estimating stock proportions was investigated in a simulation study. Results of the simulation study indicated which type of estimate was least biased. A sampling design using geographical and temporal strata was then employed to sample the Atlantic coastal fishery from Cape Hatteras, N.C., to Maine. Observations for the morphological characters were taken on collected fish and the resulting data entered into discriminant functions obtained from spawning-stock collections. The specimens were classified by area of origin and the three types of estimates of relative contribution of the Hudson, Chesapeake, and Roanoke stocks were obtained. Results indicated that the Chesapeake stock was the major contributor to the Atlantic coastal striped bass fishery and the Hudson and Roanoke stocks were minor contributors.

The striped bass, *Morone saxatilis*, is an important sport and commercial fish in the estuaries and coastal waters of the Atlantic seaboard from Maine to North Carolina (Koo 1970). Recruitment to the striped bass fishery is from various stocks of striped bass spawned and developed in rivers and estuaries along the Atlantic coast. Recapture locations of tagged striped bass indicate that individuals from all spawning areas north of Cape Hatteras, N.C., utilize much of the Atlantic coast north of their respective spawning areas during a northward migration in the spring and a southward migration in the fall (Merriman 1941; Raney et al. 1954; Alperin 1966; Schaefer 1968; Florence[3]; Texas Instruments[4]). The major spawning areas which potentially contribute individuals to the fisheries operating during the northward and southward migrations are the tributaries of Chesapeake Bay and the Roanoke and Hudson Rivers.

Although tagging data have not led to quantitative estimates of relative contribution, they have led to conflicting ideas as to which major stock of striped bass predominates in the fishery: the Hudson stock or the Chesapeake stock. Most published works have generally concluded that the striped bass stock from the Chesapeake Bay system is the major contributor to the fisheries north of Chesapeake Bay (Merriman 1941; Vladykov and Wallace 1952; Alperin 1966; Schaefer 1968; Porter and Saila[5]; Raney[6]). However, Clark[7] and Goodyear[8] concluded that the striped bass stock

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[3]Florence, B. 1974. Tag returns from 1375 large striped bass tagged in two Maryland spawning rivers. Outdoor Message. Organized Sportsmen of Mass. Oct. 1974.

[4]Texas Instruments Inc. 1976. Report on relative contribution of Hudson River striped bass to the Atlantic coastal fishery. Prepared for Consolidated Edison Company of New York, Inc., 101 p.

[5]Porter, J., and S. B. Saila. 1969. Final report for the cooperative striped bass migration study. U.S. Fish. Wildl. Serv. Contract no. 14-16-005, 33 p.

[6]Raney, E. C. 1972. The striped bass, *Morone saxatilis*, of the Atlantic coast of the United States with particular reference to the population found in the Hudson River. Testimony before USAEC Safety and Licensing Board for Indian Point, Unit no. 2. Docket no. 50-247, Oct. 30, 105 p.

[7]Clark, J. 1972. Effects of Indian Point Units 1 and 2 on the Hudson River aquatic life. Testimony before USAEC Safety and Licensing Board for Indian Point, Unit no. 2. Docket no. 50-247, Oct. 30, 63 p.

[8]Goodyear, C. P. 1974. Origin of the striped bass of the middle Atlantic coast. Testimony presented to the Committee on Merchant Marine and Fisheries of the U.S. House of Representatives. Feb. 19, 40 p.

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from the Hudson River is the major contributor to the coastal fishery from New Jersey to Massachusetts because the number of striped bass tagged in Chesapeake Bay and recaptured outside the Bay was too low to indicate a large contribution of Chesapeake stock to that fishery.

Because of the controversy of which stock predominates, we conducted a study to obtain quantitative estimates of relative percentage of the major stocks in the coastal fishery. A previous study (Grove et al. 1976) demonstrated the feasibility of using discriminant analysis on morphological characters (counts and morphometric ratios) to distinguish among Hudson, Chesapeake, and Roanoke spawning stocks of striped bass. That study showed that adequate segregation of spawning stocks within the Chesapeake Bay system was not possible. Quantitative estimates of stock composition based on morphological characters and discriminant analysis have been obtained for sockeye salmon (Fukuhara et al. 1962; Anas and Murai 1969), pink salmon (Amos et al. 1963), and Atlantic herring (Messieh 1975). The present study establishes discriminant functions based on collections of spawning-stock specimens to classify striped bass collected in the Atlantic coastal fishery from southern Maine to Cape Hatteras. The percentage of specimens collected that were classified into each stock was used to estimate the relative contribution of that stock to the fishery.

METHODS AND MATERIALS

Collection of Spawning-Stock Specimens

During the spawning season of 1975, mature striped bass were collected from the natal rivers of major stocks along the Atlantic coast. These fish were assumed to have originated from the rivers (i.e., that striped bass, like salmon and other anadromous fishes, home to their natal stream to spawn). This assumption was supported by tagging studies in which striped bass tagged on spawning grounds were recaptured on the same spawning grounds in successive years (Mansueti 1961; Nichols and Miller 1967). Collections were composed of 232 mature striped bass from the Chesapeake Bay tributaries (70 from the Rappahannock River, 53 from the Potomac River, 52 from the Choptank River, and 57 from the Elk River and Chesapeake and Delaware Canal), 168 from the Hudson River, and 99 from the Roanoke River. Only 19 sexually ripe striped bass were collected from the Delaware River above the entrance to the Chesapeake and Delaware Canal, which confirms findings by Chittenden (1971) that spawning in the Delaware River is not substantial. Therefore specimens from the Delaware River were omitted from subsequent analyses. Collections were made primarily during April in the Chesapeake Bay tributaries, Delaware and Roanoke Rivers, and during May in the Hudson River. Most specimens were obtained fresh from commercial fishermen using pound nets, haul seines, and gill nets. Some were netted by study personnel.

To assure an adequate representation of the sexes and multiple year classes in spawning-stock collections, sampling was designed to obtain nearly equal numbers of male and female striped bass and a minimum of 10 individuals in each of the following length categories: $\leq$399, 400-549, 550-699, 700-849, and $\geq$850 mm. Discriminant functions based on male and female specimens from multiple year classes are needed to analyze an oceanic population which consists of a different sex ratio and broader age structure than that of the spawning stocks.

Processing of Spawning-Stock Specimens

Scale samples, counts, measurements, sex, and state of maturity were obtained from each specimen while in fresh condition. Scale samples from above the lateral line between the first and second dorsal fins were pressed on acetate cards. Ages were determined by the scale annulus method (Mansueti 1961). Measurements from the focus to the first and second annuli were made on magnified scale images. The following counts and measurements were taken: number of lateral line scales, left pectoral rays, right pectoral rays, second dorsal rays, anal rays, upper-arm gill rakers, fork length, snout length, head length, and internostril width. Methods used were those discussed by Hubbs and Lagler (1958) and Grove et al. (1976).

Counts, measurements, and age determinations were replicated by a second observer and a set of tolerances was established to reduce observation error. When differences between replicated observations exceeded tolerances, the observations were retaken. Means of the replicated counts and means of ratios of the replicated measurements were used in subsequent analysis.

Analysis of Spawning-Stock Specimens

Choice of morphological characters for segregation of Hudson, Chesapeake, and Roanoke spawning stocks followed three stages of statistical analysis: correlation analysis between each character and fork length (FL), analysis of the effects of sex and age on each character, and discriminant analysis. Analysis involved only specimens with observations on all counts and morphometric and scale-annulus measurements.

Since spawning stocks do not include immature specimens which occur in the coastal waters, we chose only those characters that were independent (i.e., not highly correlated) of fish size and could therefore be used to segregate specimens from the entire stock. Characters were considered to be independent of length when variations (r^2) attributable to length in any stock were ≤ 0.10. Characters not independent of length were used in further analysis when the distribution of character values had small overlap among spawning stocks since such characters help identify stock origin.

Multivariate statistical tests were made to determine the effect of sex and age on the characters used to determine the discriminant functions, since one assumption of discriminant analysis was that each stock was homogeneous. Differences in character values among ages for males or females and between sexes within each stock were tested with a procedure that combined tests of equality of means and equality of covariance matrices (Anderson 1958). Assuming equal covariance matrices, rejection of the null hypotheses of equal distributions indicated that one or more of the character means differed among ages or between sexes.

Multivariate discriminant analysis was used to gain maximum separation among stocks. Linear and quadratic discriminant functions (Anderson 1958; Kendall and Stuart 1968) for each spawning stock were determined from character values obtained from collections of that stock. A stepwise procedure on the linear function was used to indicate the subset of characters which best separated the stocks. The quadratic function based on this subset was formed if the assumption of a common covariance matrix among spawning stocks needed for the linear function was not met. The assumption in discriminant analysis that characters had a multivariate normal distribution was investigated with histograms.

Ability of the discriminant functions to separate stocks and accurately estimate stock proportions was assessed using functions based on total spawning-stock collections and functions obtained from a cross-validation procedure (Mosteller and Tukey 1968). In this procedure collections were randomly divided in half and discriminant functions were determined from one-half and applied to each half. Percentages of correct classification and estimates of stock proportion were obtained for each subset and compared with those from the total sample. Comparisons were also made between estimated and known spawning-stock percentages.

Although these estimates of stock percentages may accurately approximate true percentages in spawning-stock collections, they may deviate substantially from stock percentages in oceanic collections. Fukuhara et al. (1962) stated that the bias in these estimates increased as stock percentages became more disproportionate. Since stock percentages in oceanic collections may be more disproportionate than stock percentages in spawning-stock collections (i.e., 34% Hudson, 46% Chesapeake, and 20% Roanoke stocks), less biased estimates of stock percentages may be needed.

Adjusting Estimates of Stock Percentages

Two procedures were developed to obtain estimates of stock percentages that were less biased than the as-classified (i.e., classifications obtained directly from discriminant functions) estimates. The first procedure adjusted estimates using a technique described by Worlund and Fredin (1962) which generalized to the three population case methodology developed in Fukuhara et al. (1962). This procedure used percentages of specimens from each spawning stock that were misclassified into other stocks to correct as-classified estimates for bias due to misclassifications. When adjusted estimates were negative, as-classified estimates were modified by methodology developed by Schuermann and Curry.[9]

The second procedure iteratively reclassified specimens based on updated prior probabilities that specimens originated from each of the spawning stocks. The first stage of the procedure is the same as the as-classfied procedure; therefore as-

[9]Schuermann, A. C., and G. L. Curry. 1973. Notes on parametric programming. Unpubl. manuscr. Dep. Ind. Eng. Texas A&M Univ., College Station.

classified estimates of stock contribution are obtained at the end of this stage. However, these estimates are then used in the second stage as prior probabilities that specimens come from the three stocks. For example, the as-classified estimate of Hudson stock contribution obtained at the end of the first stage was used at the beginning of the second stage as our best guess of the proportion of specimens in the sample that originate from the Hudson. These prior probabilities are then used to weight the decision to classify each specimen into one of the stocks. Similarly, the proportion of specimens classified into each stock in the second stage were used as priors in the third stage. The procedure was carried out for nine stages.

The effectiveness of adjusted and iterative estimates in reducing bias in the as-classified estimate due to misclassification was investigated in a simulation study. Discriminant functions from the cross-validation study were used to classify a subset of specimens from the independent half of the spawning-stock collections, and each of the three types of estimates of relative percentage were obtained and compared with the known stock percentage. For percentages of Hudson stock ranging from 0 to 90%, the difference between each estimate of Hudson percentage and the known percentage of Hudson specimens in the subsample was obtained as a measure of bias in the estimate.

Collection, Processing, and Analysis of Atlantic and Hudson River Specimens

Assessment of the relative contribution of various stocks of striped bass to the Atlantic coastal fishery required a stratified sampling design that provided samples from the entire coastal fishery and considered the migratory nature of striped bass; therefore a geographically and temporally stratified sampling design was used. The geographical stratification consisted of 10 strata from southern Maine to Cape Hatteras, with 2 to 4 substrata within each stratum to compensate for variations in stock composition within the stratum (Figure 1). The Rhode Island stratum was not subdivided because of its small size. Temporally, the year was divided into six 2-mo periods to obtain estimates of stock composition by stratum throughout the year.

Collections of striped bass from the coastal fishery were obtained primarily from sport and commercial fishermen; however, in areas where adequate sport and commercial fisheries did not exist, study personnel used haul seines and gill nets to collect specimens. Collections were limited to striped bass caught during the same day (i.e., within 24 h) to assure freshness. In many instances the entire catch was used, but due to the size of some catches, a random sample proportional to the number of small (<550 mm), medium (550-850), and large (>850) striped bass caught was obtained.

Oceanic and overwintering specimens were processed in the same manner as spawning-stock specimens. Two replicates of 10 counts and measurements were taken from each specimen, and scale samples were obtained for subsequent age and growth rate determinations in the laboratory. A total of 2,737 oceanic specimens with a complete set of meristic, morphometric, and scale characters were processed (Table 1). Additionally, 79 striped bass overwintering in Croton Bay on the

TABLE 1.—Number of striped bass with complete character sets[1] collected by spatial stratum and period from Atlantic coastal fishery in 1975.

Spatial stratum	Locality	Legal/ sublegal[2]	Jan.-Feb.	Mar.-Apr.	May-June	July-Aug.	Sept.-Oct.	Nov.-Dec.	Total
1	S. Maine-N. Mass.	Legal			82	58	74		214
2	S. Mass.	Legal			91	90	82		263
3	Rhode Is.	Legal			60	43	56		159
4	E. Long Is. Sound	Legal			96		140	99	335
		Sublegal			5			1	6
5	W. Long Is. Sound	Legal	1	38	14	15	89		157
		Sublegal		2	42	85	10		139
6	E. Long Is. S. Shore	Legal		1	89	102	86	106	384
		Sublegal			8	17	19		44
7	W. Long Is. S. Shore	Legal		30	58	93	120	124	425
		Sublegal		4	11				15
8	N.J.	Legal		34	113	28	73	117	365
9	Del.-Md.-N. Va.	Legal		71	3		6	100	180
10	S. Va.-N.C.	Legal	27					24	51
Total			28	180	672	531	755	571	2,737

[1]Measurements and counts taken on all variables used in the character set.
[2]Sublegal-sized striped bass (<406.5 mm FL) from New York waters (strata 4 to 7) were analyzed separately.

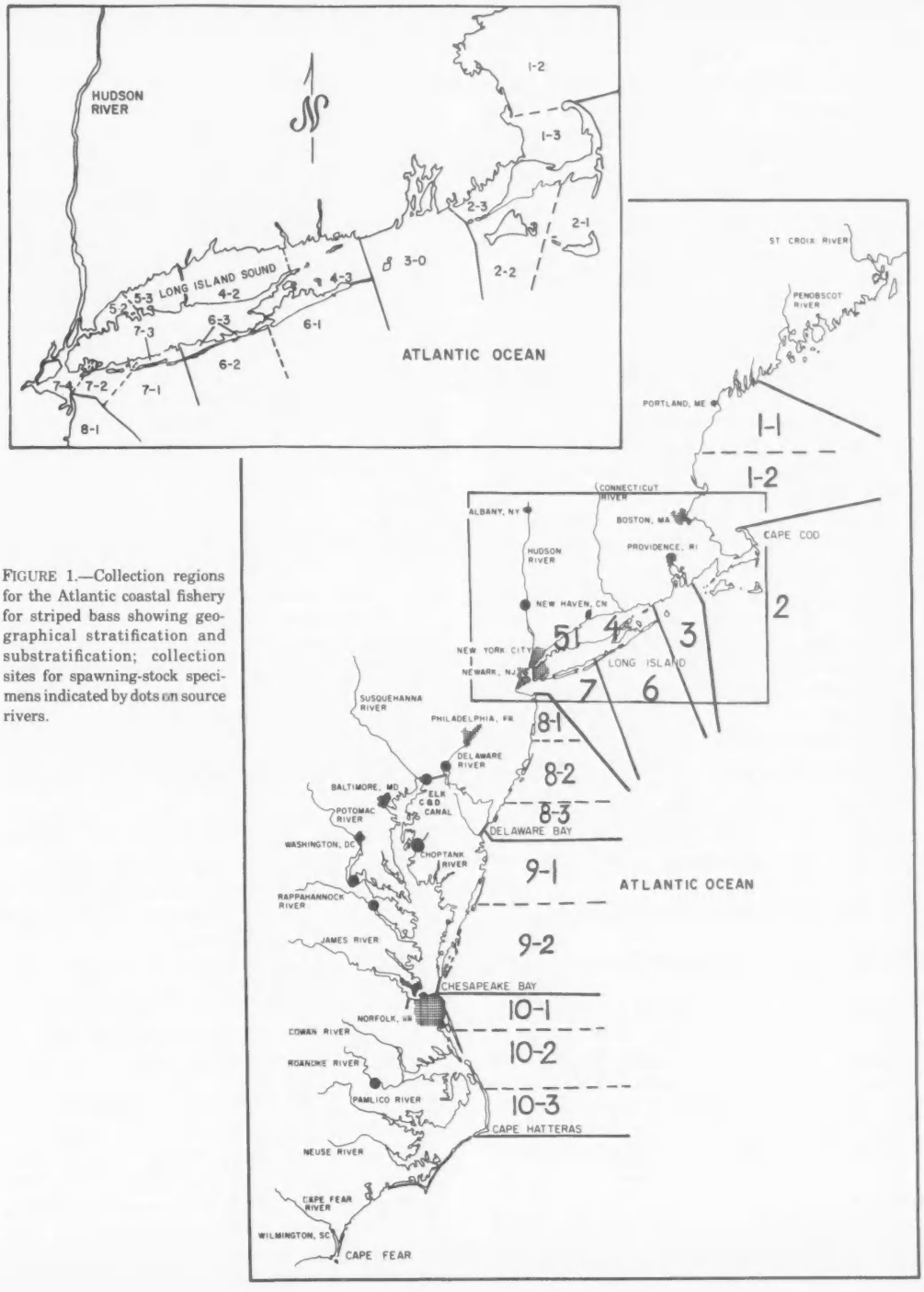

FIGURE 1.—Collection regions for the Atlantic coastal fishery for striped bass showing geographical stratification and substratification; collection sites for spawning-stock specimens indicated by dots on source rivers.

Hudson River from 6 December 1974 through 20 March 1975 were processed.

Three estimates of stock contribution, i.e., "as-classified," "adjusted," and "iterative" estimates, were calculated for collections of legal-sized, sublegal-sized, and overwintering striped bass by geographical and temporal strata. Sublegal-sized <406.5 mm or 16 in FL) and overwintering striped bass collected in New York waters were not considered to be a part of the coastal fishery and were analyzed separately. In each stratum, the percentage of striped bass allocated to a stock provided an estimate of that stock's relative contribution. Mean 1975 estimates of stock contribution of legal-sized striped bass were calculated by averaging strata estimates within periods then averaging across the six periods. Relative contribution estimates by age were also obtained.

The influence of the Hudson stock in coastal strata adjacent to the Hudson River was investigated by comparing the relative contribution of Hudson, Chesapeake, and Roanoke stocks within "inner" and "outer" zones designed by the U.S. Nuclear Regulatory Commission.[10] The inner zone encompassed western Long Island Sound (stratum 5), the New York Bight (stratum 7), and northern New Jersey (stratum 8-1), whereas the outer zone encompassed the remaining waters from Cape May, N.J., to Maine (strata 1 to 4, 6, 8-2, 8-3). Estimates of relative contribution for inner and outer zones were calculated for each period by summing the number of Hudson-, Chesapeake-, and Roanoke-classified fish within appropriate strata. Mean estimates of contribution within each zone were calculated for the year by averaging across temporal strata.

RESULTS AND DISCUSSION

Establishment of Discriminant Functions

Five characters were established as the character set best able to discriminate among Hudson, Chesapeake, and Roanoke stocks. They are, in order of importance (as established by stepwise linear discriminant analysis): 1) the ratio of snout length/internostril width, 2) the scale ratio of first to second annulus/focus to first annulus measure, 3) a character index (Raney and deSylva 1953), 4) the upper-arm gill raker count (which includes rudimentary rakers), and 5) the lateral line scale count. The character index, i.e., the sum of left and right pectoral, second dorsal, and anal fin rays, was used since Grove et al. (1976) demonstrated that individual fin ray characters did not add significant discriminatory ability.

The five characters satisfied the criterion for independence with fish length in each stock with only one exception. The snout length/internostril width ratio for the Roanoke stock has a coefficient of determination of nearly 0.20 but was retained because its distribution had the least overlap among spawning stocks of all characters, thus making it a potentially good discriminator.

Results of the test of homogeneity indicated that only the Hudson stock was homogeneous among ages and between males and females. Significant differences ($\alpha = 0.05$) were found among ages and between sexes in the Chesapeake spawning stock and among ages in the Roanoke spawning stock. Differences found in the Chesapeake spawning stock may have resulted from pooling collections from its four major tributaries.

Quadratic functions (Table 2) were used to discriminate among stocks as a result of the investigation of underlying assumptions of discriminant analysis. Significant differences ($\alpha = 0.05$) were found among covariance matrices of Hudson, Chesapeake, and Roanoke spawning stocks which suggested that quadratic functions would better discriminate among these stocks than linear functions. Histograms suggested that no radical departure of multivariate normality was evident, although normality of individual characters does not assure multivariate normality of the character set. Therefore multivariate normality of the character sets was assumed.

Percentage of spawning-stock specimens correctly classified by the quadratic functions and estimated stock percentages resulting from the use of these functions closely agreed with results obtained by the cross-validation procedure (Table 3). For the total set of collections, 76.8% of Hudson specimens, 67.7% of Chesapeake specimens, and 85.9% of Roanoke specimens were correctly classified, resulting in an overall correct classification of 74.4%. This was similar to overall percentages of 73.2 and 77.1 obtained for the cross-validation subsets. Estimated relative percentages for each stock varied <3 percentage points among the total set and cross-validated subsets, whereas varia-

[10]U.S. Nuclear Regulatory Commission. 1975. Final environmental statement related to operation of Indian Point Nuclear Generating Plant Unit no. 3 Consolidated Edison Company of New York, Inc. Office of Nuclear Reactor Regulation. Docket no. 50-286, Vol. 1:V-166-V-178.

TABLE 2.—Quadratic discriminant functions[1] based on Hudson, Chesapeake, and Roanoke spawning-stock specimens of striped bass and used to classify spawning-stock, oceanic, and overwintering specimens.[2]

Hudson:

$$F_{HUD} = -1{,}489.070559 - (0.077516\,U^2 + 0.256954\,W^2 + 1.171065\,X^2 + 2.536320\,Y^2 + 123.907000\,Z^2 - 0.019058\,UW + 0.015160\,UX - 0.007057\,UY + 0.090968\,UZ + 0.047441\,WX + 0.023246\,WY + 0.164200\,WZ + 0.457365\,XY - 2.799760\,XZ - 2.861250\,YZ) + 8.776221\,U + 28.127772\,W + 24.321052\,X + 7.985031\,Y + 381.695141\,Z.$$

Chesapeake:

$$F_{CHES} = -1{,}368.946420 - (0.089560\,U^2 + 0.242459\,W^2 + 1.122690\,X^2 + 2.155850\,Y^2 + 117.554000\,Z^2 - 0.007099\,UW + 0.005302\,UX + 0.015500\,UY + 0.321075\,UZ - 0.092151\,WX - 0.000861\,WY - 2.363980\,WZ + 0.381082\,XY + 3.623860\,XZ - 1.590090\,YZ) + 11.316822\,U + 21.749040\,W + 25.294896\,X + 7.014936\,Y + 323.469441\,Z.$$

Roanoke:

$$F_{ROAN} = -1{,}650.902863 - (0.107062\,U^2 + 0.316254\,W^2 + 2.063540\,X^2 + 0.842590\,Y^2 + 139.577500\,Z^2 - 0.062826\,UW + 0.015703\,UX + 0.043640\,UY + 0.228873\,UZ - 0.293615\,WX + 0.129292\,WY - 1.009790\,WZ + 0.106776\,XY - 0.606466\,XZ + 4.416000\,YZ) + 10.320202\,U + 27.000888\,W + 25.512087\,X + 22.351388\,Y + 469.422957\,Z.$$

[1]Except for an additive constant ($-2.5 \ln 2\pi$) common to each function.
[2]F = discriminant score, U = lateral line scale count, W = character index, X = upper-arm gill raker count, Y = first to second annulus/focus to first annulus measurement ratio, and Z = snout length/internostril width ratio.

TABLE 3.—Comparison of correct-classification percentages and estimated and known stock percentages among the total set of spawning-stock specimens of striped bass and cross-validation subsets.

	Random set[1]			Independent set[2]			Total set[3]		
Spawning stock	Correctly classified (%)	Known stock (%)	Estimated stock (%)	Correctly classified (%)	Known stock (%)	Estimated stock (%)	Correctly classified (%)	Known stock (%)	Estimated stock (%)
Hudson	81.0	33.7	36.5	72.6	33.6	35.2	76.8	33.7	36.9
Chesapeake	69.8	46.6	40.2	68.1	46.4	42.4	67.7	46.5	40.3
Roanoke	87.8	19.7	23.3	86.0	20.0	22.4	85.9	19.8	22.9
Overall	77.1			73.2			74.4		

[1]Randomly sampled half of total spawning-stock collections used to determine quadratic functions for cross-validation.
[2]Remaining half of spawning-stock specimens classified by quadratic functions based on the random set.
[3]All specimens from spawning-stock collections classified by quadratic functions based on the total set.

tions between estimated and known stock percentages within sets was as much as 9 percentage points. The quadratic functions thus provided slightly biased estimates of stock percentages when applied to collections composed of 34% Hudson, 46% Chesapeake, and 20% Roanoke stocks.

Best Estimator of Relative Contribution

The best estimate of the percentage of Hudson River specimens in subsamples from the simulation studies was the estimate from the third iteration of the reclassification procedure (Table 4). On the average, this iterative estimate was less biased than estimates from other iterations, the as-classified estimated (i.e., estimate from the first iteration), and the adjusted estimate for most percentages of Hudson stock considered. In addition, the variance of the bias of the iterative estimate was often less than that of the other estimates. For percentages of Hudson stock $\leq 50\%$, the iterative and adjusted estimates closely agreed and the bias in each estimate was small (≤ 5 percentage points). The iterative estimate will, therefore, be used to estimate Hudson stock contribution in oceanic collections, and the adjusted estimate will be used to substantiate estimates of Hudson contribution $\leq 50\%$. The iterative estimate will also be used to estimate Chesapeake and Roanoke stock contributions.

TABLE 4.—Mean and standard deviation of absolute bias[1] of estimated relative percentages of Hudson River stock of striped bass in replicated random samples from spawning-stock collections.[2]

Known percent of Hudson River stock	Estimates of absolute bias					
	As-classified		Iterative		Adjusted	
	Mean	SD	Mean	SD	Mean	SD
[3]90	23.0	2.40	4.3	2.97	14.4	5.73
80	20.2	5.14	7.4	8.82	14.3	7.78
75	17.6	3.47	8.4	3.82	12.8	5.00
70	13.0	3.32	4.7	4.52	7.3	4.80
65	10.8	3.11	3.3	2.98	7.5	4.07
60	9.0	3.21	5.3	2.84	6.8	5.00
55	7.5	2.95	4.8	3.52	7.4	4.02
50	5.5	1.99	4.2	2.66	4.7	3.44
45	2.2	2.17	3.5	1.85	4.7	2.14
40	1.2	1.04	3.2	3.44	4.3	4.21
35	2.2	1.45	[4]4.2	[4]2.09	4.4	2.87
30	5.9	3.18	3.3	2.43	3.4	1.79
25	7.8	3.07	4.0	2.25	4.2	3.27
20	9.5	2.26	2.8	1.72	1.8	0.99
15	12.1	4.19	3.5	3.24	3.3	2.62
10	15.1	3.80	4.5	3.36	5.0	3.61
5	17.4	4.03	4.5	3.72	4.3	3.85
0	18.1	2.53	2.5	1.73	1.5	1.69
Overall mean	11.0		4.4		6.2	

[1]Absolute value of the difference between the true relative percentage of Hudson River stock in the subsample and the estimated relative percentage based on nine replicates of varying Chesapeake and Roanoke proportions in the subsamples.
[2]Estimates were based on random samples from one-half of spawning-stock collections which were classified as to area of origin by quadratic functions obtained from the other half of the collections.
[3]Based on two replicates.
[4]Based on eight replicates.

Estimates of Stock Contribution for Oceanic and Overwintering Collections

Iterative estimates of relative contribution of Hudson, Chesapeake, and Roanoke stocks indicated that the Chesapeake stock was the major contributor to the striped bass fishery along the Atlantic coast while the Hudson and Roanoke stocks were minor contributors (Table 5). The Chesapeake stock predominated in 34 of 35 geographical and temporal strata while the Hudson stock predominated in the remaining stratum. Iterative estimates of Chesapeake contribution to the fishery exceeded 80% in all strata not adjacent to the Hudson River. Iterative estimates of the Hudson stock were largest in western Long Island Sound and the New York Bight with values exceeding 20% during some periods. Although iterative estimates of Roanoke stock contribution never exceeded 20%, they were highest in North Carolina waters (stratum 10) and in strata from Massachusetts to Maine (strata 1, 2).

The Hudson stock contribution in strata from Massachusetts north to Maine and from New Jersey south to North Carolina (strata 8 to 10) should be low as indicated by iterative estimates (Table 5) and results of tagging studies. Zero estimates in northern waters do not necessarily indicate an absence of Hudson River striped bass since the simulation study has shown that such estimates may be obtained in situations where true contribution is low. In fact, data on adult striped bass tagged in the Hudson River during spawning season and recaptured in waters as far north as Boston Harbor, Mass., have indicated a northern migration of a portion of the Hudson stock (Texas Instruments see footnote 4). However, these data support near-zero estimates of Hudson contribution in southern waters since tagged striped bass were not recaptured south of northern New Jersey. Data (Chapoton and Sykes 1961) on adult striped bass tagged along the outer coast of North Carolina and recaptured on the spawning grounds of Chesapeake Bay and Albemarle Sound

TABLE 5.—Estimates of relative contribution of Hudson, Chesapeake, and Roanoke stocks of legal-sized striped bass[1] to 1975 oceanic collections by period and spatial strata. As-cl. = As-classified, Iter. = Iterative, and Adj. = Adjusted estimates.

Period	Stratum	Sample size[2]	Hudson			Chesapeake			Roanoke		
			As-cl.	Iter.	Adj.	As-cl.	Iter.	Adj.	As-cl.	Iter.	Adj.
Jan.-Feb.	10	27	25.9	3.7	6.7	63.0	92.6	90.7	11.1	3.7	2.6
Mar.-Apr.	5	38	52.6	57.9	54.2	42.1	42.1	45.8	5.3	0.0	0.0
	7	30	23.3	3.3	0.0	73.3	96.7	100.0	3.3	0.0	0.0
	8	34	23.5	8.8	0.8	67.6	88.2	99.2	8.8	2.9	0.0
	9	71	8.5	0.0	0.0	77.5	97.2	98.9	14.1	2.8	1.1
May-June	1	82	11.0	0.0	0.0	68.3	90.2	88.5	20.7	9.8	11.5
	2	91	14.3	0.0	0.0	71.4	95.6	96.4	14.3	4.4	3.6
	3	60	30.0	3.3	13.9	60.0	96.7	84.5	10.0	0.0	1.6
	4	96	21.9	1.0	0.0	69.8	99.0	100.0	8.3	0.0	0.0
	5	14	35.7	28.6	23.0	57.1	71.4	77.0	7.1	0.0	0.0
	6	89	25.8	5.6	5.4	65.2	93.3	94.6	9.0	1.1	0.0
	7	58	41.4	25.9	33.7	51.7	70.7	66.3	6.9	3.4	0.0
	8	113	23.9	0.0	1.5	67.3	100.0	98.5	8.8	0.0	0.0
July-Aug.	1	58	19.0	0.0	0.0	67.2	94.8	95.4	13.8	5.2	4.6
	2	90	7.8	0.0	0.0	72.2	96.7	90.8	20.0	3.3	9.2
	3	43	30.2	2.3	10.3	65.1	97.7	89.7	4.7	0.0	0.0
	5	15	26.7	0.0	5.1	66.7	100.0	94.9	6.7	0.0	0.0
	6	102	22.5	7.8	1.6	63.7	88.2	92.7	13.7	3.9	5.7
	7	93	33.3	15.1	13.4	65.6	84.9	86.6	1.1	0.0	0.0
	8	28	21.4	0.0	0.0	71.4	100.0	100.0	7.1	0.0	0.0
Sept.-Oct.	1	74	13.5	0.0	0.0	77.0	98.6	100.0	9.5	1.4	0.0
	2	82	12.2	0.0	0.0	58.5	85.4	76.0	29.3	14.6	24.0
	3	56	25.0	3.6	7.5	58.9	94.6	83.3	16.1	1.8	9.2
	4	140	16.4	0.7	0.0	64.3	94.3	88.6	19.3	5.0	11.4
	5	89	41.6	40.4	37.2	46.1	57.3	56.5	12.4	2.2	6.4
	6	86	15.1	0.0	0.0	73.3	96.5	99.8	11.6	3.5	0.2
	7	120	23.3	1.7	2.9	63.3	95.0	91.6	13.3	3.3	5.2
	8	73	16.4	0.0	0.0	76.7	98.6	100.0	6.8	1.4	0.0
	9	6	16.7	0.0	0.0	66.7	100.0	92.2	16.7	0.0	7.8
Nov.-Dec.	4	99	21.2	0.0	0.0	66.7	98.0	96.9	12.1	2.0	3.1
	6	106	16.0	0.0	0.0	69.8	99.1	95.9	14.2	0.9	4.1
	7	124	21.0	4.8	0.0	76.6	95.2	100.0	2.4	0.0	0.0
	8	117	21.4	0.0	0.0	72.6	100.0	100.0	6.0	0.0	0.0
	9	100	8.0	0.0	0.0	80.0	99.0	100.0	12.0	1.0	0.0
	10	24	12.5	0.0	0.0	62.5	83.3	82.0	25.0	16.7	18.0
Overall mean			23.0	6.5	6.6	66.0	90.8	90.2	11.0	2.7	3.2

[1]Not included are striped bass <406.5 mm FL from New York waters.
[2]Sample sizes of five specimens or less in any stratum are not included.

tributaries also support near-zero estimates of Hudson River contribution in waters off North Carolina.

Comparison between iterative and adjusted estimates indicated close agreement for each stock within the 35 strata. The largest difference between estimates was 12.2 percentage points, but differences of <5 percentage points occurred in 80% of the strata for the Hudson stock, 71% of the strata for the Chesapeake stock, and 86% of the strata for the Roanoke stock. The adjusted estimates therefore substantiate low iterative estimates of contribution of Hudson and Roanoke stocks.

Comparison of mean iterative and adjusted estimates of relative contribution indicated that the two estimates differed by <1 percentage point for each stock. Mean iterative and adjusted estimates were, respectively, 6.5 and 6.6% Hudson, 90.8 and 90.2% Chesapeake, and 2.7 and 3.2% Roanoke contribution.

The contribution of the Hudson stock to the coastal fishery was greater in strata adjacent to the Hudson River than in the remaining strata. Mean iterative estimates of relative contribution of the Hudson River stock to inner and outer zones were 16.0% (15.0% adjusted) and 2.8% (0.0% adjusted), respectively, for the year (Table 6). Although the Chesapeake stock was the predominant contributor to both inner and outer zones, the contribution of the Hudson stock exceeded that of the Roanoke stock in the inner zone but was less in the outer zone.

The Hudson stock predominated in collections of sublegal-sized striped bass in western Long Island Sound, the New York Bight, and in collections of specimens overwintering in Croton Bay on the Hudson River (Table 7). Iterative (and adjusted) estimates of the percentage of sublegal-sized fish classified into the Hudson stock in western Long Island Sound (primarily in Little Neck Bay) and the New York Bight were at least 80%, but were less than 40% along the southeastern shore of Long Island (stratum 6) from May through October. The iterative (and adjusted) estimated of contribution of the Hudson stock to the overwintering population in the Hudson River was greater than 95%.

This study has provided additional information in the importance of dominant year classes of striped bass. Approximately 52% of the specimens collected from the coastal fishery in 1975 were from the 1970 year class, and 77% of them were classified as Chesapeake fish. Schaefer (1972) stated that production of young-of-the-year striped bass in Chesapeake Bay during 1970 was the largest ever recorded and that this year class should provide excellent fishing in New York waters for 6 to 8 yr after recruitment. The presence of this dominant year class of Chesapeake fish confirms the rationale used by Merriman (1941) and Schaefer (1968) to conclude that the Chesapeake stock predominates in the coastal fishery. A summary of the occurrence of dominant year classes in the Atlantic coastal fishery has been given by Schaefer (1968).

TABLE 6.—Mean estimates[1] of relative contribution of Hudson, Chesapeake, and Roanoke stocks of legal-sized striped bass[2] to 1975 oceanic collections within USNRC zones.[3]

	Inner zone			Outer zone		
Estimate	Hudson	Chesapeake	Roanoke	Hudson	Chesapeake	Roanoke
As-classified	31.7	62.9	5.5	19.2	68.0	12.8
Iterative	16.0	83.1	0.9	2.8	94.2	3.0
Adjusted	15.0	84.2	0.8	0.0	96.4	3.6

[1]Average of five temporal strata since only one striped bass collected in inner zone during period 1 (Jan.-Feb.).
[2]Not included are striped bass <406.5 mm FL from New York waters.
[3]U.S. Nuclear Regulatory Commission inner zone corresponds to study strata 5, 7, and 8-1; the outer zone corresponds to study strata 1 to 4, 6, 8-2, and 8-3.

TABLE 7.—Estimates of relative contribution of Hudson, Chesapeake, and Roanoke stocks of sublegal-sized striped bass[1] to New York waters by period and spatial stratum and of legal-sized striped bass to the overwintering population in the Hudson River. As-cl. = as-classified, Inter. = iterative, and Adj. = adjusted estimates.

				Hudson			Chesapeake			Roanoke		
Population	Period	Stratum	Sample size[2]	As-cl.	Iter.	Adj.	As-cl.	Iter.	Adj.	As-cl.	Iter.	Adj.
Overwintering			76	76.3	97.4	95.7	23.7	2.6	4.3	0.0	0.0	0.0
Sublegal	May-June	5	42	92.9	100.0	100.0	7.1	0.0	0.0	0.0	0.0	0.0
		6	8	12.5	0.0	0.0	50.0	62.5	64.3	37.5	37.5	35.7
		7	11	81.8	81.8	100.0	18.2	18.2	0.0	0.0	0.0	0.0
	July-Aug.	5	85	88.2	100.0	100.0	11.8	0.0	0.0	0.0	0.0	0.0
		6	17	41.2	35.3	39.2	41.2	58.8	47.4	17.6	5.9	13.4
	Sept.-Oct.	5	10	80.0	80.0	100.0	20.0	20.0	0.0	0.0	0.0	0.0
		6	19	26.3	15.8	20.8	36.8	47.4	41.9	36.8	36.8	37.3

[1]Striped bass <406.5 mm FL from New York waters.
[2]Sample sizes of five specimens or less in any stratum are not included. Three sublegal-sized specimens collected overwintering in the Hudson River were classified as Hudson fish.

SUMMARY AND CONCLUSIONS

A study was conducted to identify the origin of striped bass collected in the Atlantic coastal fishery and estimate the relative contribution of major stocks to the fishery. Quadratic discriminant analysis was applied to values of five morphological characters obtained from Hudson, Chesapeake, and Roanoke spawning-stock specimens to determine functions which best separated the stocks. Correct-classification percentages of 76.8, 67.7, 85.9% were obtained for the Hudson, Chesapeake, and Roanoke spawning stocks, respectively, resulting in an overall correct classification of 74.4% of the specimens.

A simulation study was conducted to investigate the bias in as-classified, iterative, and adjusted estimates of relative contribution due to misclassification error inherent in the discriminant functions. Results indicated that iterative estimates may best approximate the true contribution of the Hudson stock in oceanic collections.

A stratified sampling design was used during six 2-mo periods in 1975 to collect representative samples of striped bass in the Atlantic coastal fishery from southern Maine to Cape Hatteras. This provided estimates of stock composition by stratum throughout the year.

Oceanic samples were classified by discriminant functions and as-classified, iterative, and revised estimates of relative contribution of the major stocks were obtained. Mean iterative estimates of relative contribution for 1975 are 6.5% Hudson, 90.8% Chesapeake, and 2.7% Roanoke stocks. Iterative estimates of Hudson contribution for legal-sized striped bass exceeded 20% only in western Long Island Sound and the New York Bight during certain months. In collections from Western Long Island Sound and the New York Bight, iterative estimates of the percentage of sublegal-sized fish classified into the Hudson stock were at least 80% during the May through October periods. For Hudson River collections of overwintering striped bass, an iterative estimate of 97.4% Hudson stock was obtained.

The occurrence of a dominant year class was noted. Approximately 52% of the legal-sized specimens collected in the 1975 oceanic sampling program were from the 1970 year class, and 77% of these were classified as Chesapeake in origin.

Major conclusions drawn from the study are: 1) the Chesapeake stock is the major contributor to the Atlantic coastal striped bass fishery from southern Maine to Cape Hatteras; 2) the Chesapeake stock is also the major contributor of legal-sized striped bass in the vicinity of the Hudson River (western Long Island Sound and the New York Bight); 3) sublegal-sized striped bass collected in the vicinity of western Long Island Sound and the New York Bight are predominantly of Hudson origin; and 4) striped bass overwintering in the Hudson River are predominantly of Hudson origin.

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COPPER SENSITIVITY OF PACIFIC HERRING, *CLUPEA HARENGUS PALLASI*, DURING ITS EARLY LIFE HISTORY

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ABSTRACT

Embryos and larvae of the Pacific herring, *Clupea harengus pallasi*, were exposed to copper, using a flow-through bioassay system. Herring embryos were exposed continuously from 12 h after fertilization until hatching, and larvae were exposed from the time of hatching until yolk sac absorption. Embryos were also exposed to 36-h duration pulses of copper in order to evaluate the sensitivy of different developmental stages of herring embryos to copper. Pulsed exposures started at 62, 98, or 136 h after fertilization. The following measurements were taken as indices of the toxic effects of copper: cumulative mortality, percent hatching, and larval length upon hatching.

The onset of mortality of herring embryos continuously exposed to copper began 90 h after fertilization, with deaths occuring over a short interval thereafter (response period). Significant embryo mortalities occurred at a copper concentration as low as 35 μg/l. Herring larvae continuously exposed to copper showed significant mortality at 300 μg/l copper, with no delay in the onset of mortality. Embryos exposed to 36-h pulses of copper during different developmental stages showed reduced sensitivity when exposed after the response period. Larvae that hatched from eggs exposed to a 36-h pulse of copper before the response period grew significantly less than those hatched from eggs exposed during later developmental stages.

Numerous studies have shown that many aquatic animals are adversely affected by increased levels of copper in water; most of the work on fishes has been restricted to freshwater species (Becker and Thatcher 1973; Brungs et al. 1976). Since 90% of the world's marine fish are taken from the continental shelf and nearshore upwelling areas (Waldichuk 1974), increases in copper pollution in coastal aquatic ecosystems are of particular concern.

The concentration of copper in unpolluted nearshore waters ranges from 0.3 to 3.8 μg/l (Chester and Stoner 1974). Increased concentrations of copper in coastal waters have resulted from the release of municipal waste waters (Mytelka et al. 1973; Mitchell and McDermott 1975) and of effluents from power plants (Hoss et al. 1975; Martin et al. 1977). In polluted waters, concentrations as high as 13,900 μg/l copper have been reported (Mitchell and McDermott 1975).

Examination of the toxic effects of copper on coastal marine fisheries is important for the establishment of water quality standards that will protect fishery resources of coastal zones. Eggs and larval stages of fish are reported to be the life history stages that are most sensitive to a variety of pollutants (Skidmore 1965; Pickering and Gast 1972; Struhsaker et al. 1974; Christensen 1975). The necessity of conducting toxicity tests during the most susceptible stage in the life history of an organism has been emphasized by Hynes (1970), and the sensitivity of vertebrate embryos to heavy metals has been suggested as a criterion for water quality by Birge and Just (1973).

While some work has been done to assess the toxicity of copper to the early life history stages of freshwater fishes (Mount 1968; Hazel and Meith 1970; McKim and Benoit 1971; O'Rear 1972; Gardner and La Roche 1973; Benoit 1975), little assessment has been made of toxic effects of copper on marine fishes. Such studies should be very important since mortalities that occur during the early life history stages of marine fish strongly influence the strength of a given year class of fish (May 1974; Bannister et al. 1974; Postuma and Zijlstra 1974; Cushing 1975; Vaughan and Saila 1976). Toxic effects that have an impact upon survival during early developmental stages would also act to reduce the strength of a given year class of fish. The embryos and larvae of the Pacific herring, *Clupea harengus pallasi*, represent a useful

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test organism for evaluating the toxic effect of copper upon the early life history stages of marine fish. The Pacific herring is a commercially important fish that spawns along both eastern and western Pacific coasts (Eldridge and Kail 1973; Hart 1973). Herring spawn great numbers of demersal, adhesive eggs on shallow intertidal substrates. The egg is relatively large, 1.3 to 1.6 mm in diameter, and is covered by a thick, three-layered, opaque chorion (Blaxter and Holliday 1963). Development of the embryo is comparatively slow, taking 7 to 9 days at 14°C (Alderdice and Velsen 1971). The tough chorion permits easy collection and handling, and the slow development of the embryo allows observation time not available in more rapidly developing species.

Three bioassays were conducted to evaluate the sensitivity of herring embryos and larvae to copper. The first two assays were designed to evaluate the sensitivity of embryos and larvae to continuous copper exposure, while the third examined the sensitivity of embryos to brief copper exposures. Since the form of copper to which the herring embryos and larvae were exposed may play a significant role in the toxic response (Pagenkopf et al. 1974), the partitioning of copper among the components of the water in the bioassay system was also determined.

MATERIALS AND METHODS

Collection and Handling of Test Organisms

Intertidal collections of Pacific herring eggs were made along the shore of Belvedere Island and the Tiburon Peninsula, San Francisco Bay, Calif. The eggs were collected directly into a 15-gal, insulated ice chest containing aerated seawater from the egg collection site and were transported to the laboratory within 2 h after collection. The water temperature at the collection site was 11.0°-11.5°C and upon arrival at the laboratory the temperature of the water increased to no more than 13.5°C. Only eggs deposited in single layers on *Fucus* sp., *Laminaria* sp., or *Gracilaria* sp. were chosen for testing. Before placing the eggs into exposure chambers, they were removed from the seaweed by bending the frond and then gently brushing them with a finger into a sorting dish containing seawater kept at 12°C. The eggs were examined with a microscope at 20×; only viable embryos at the same stage of development were chosen. No more than 51 embryos were placed in any exposure chamber. All transfers of embryos or larvae were carried out with a large-bore, polished glass pipette.

Embryos at two different stages of development were used for the tests. The age of the earlier stage embryos, collected 7 February 1975, was estimated to be 12 h after fertilization since they were undergoing epiboly (Ahlstrom's stage IV (Ahlstrom 1943)). These embryos were exposed to copper continuously, each of seven groups being exposed to a different copper concentration. The age of the later stage embryos, collected 26 February 1975, was estimated to be 48 to 50 h after fertilization (Ahlstrom's stage IX). These embryos were divided into four groups. Three groups were exposed for 36 h to the same copper concentration but during different developmental stages. The fourth group was maintained in flowing seawater from the time of collection to within 1 h after hatching, and then continuously exposed to different copper concentrations as larvae.

Bioassay System

The organisms were exposed to copper in 5-l clear plastic bowls (Figure 1). The exposure solution was introduced into each chamber by gravity flow from a mixing chamber into which seawater, at a rate of 11 ml/min, and copper chloride solution, pH 3, at a rate of 1 ml/h, were pumped continuously. Approximately 17 h was required for replacement of 90% of the water in the chamber. The height of water in the exposure chambers was maintained by a constant-level out-flow siphon. The diameter of the mouth of the out-flow siphon

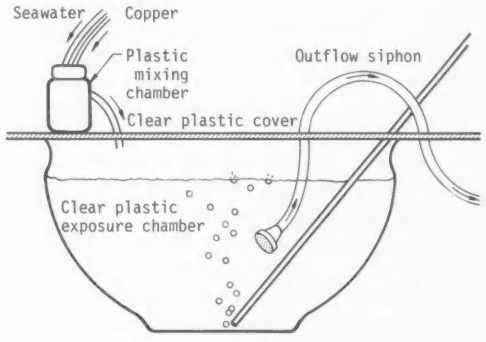

FIGURE 1.—Diagram of the exposure chamber and flow-through delivery system used to expose Pacific herring embryos and larvae to copper.

was greater than that of the tubing to reduce the flow velocity at the mouth of the siphon. The mouth of the siphon was covered with nylon netting (505-μm pore size) to prevent the loss of organisms from the chamber. A gentle stream of bubbles delivered to the bottom of the chamber provided aeration and mixing. All exposure chambers were immersed in a water bath whose temperature was monitored. Illumination was provided by the fluorescent lighting in the laboratory and followed the regular ambient photoperiod.

The exposure period, the nominal copper concentration, and the total number of embryos or larvae exposed during a typical experiment are given in Table 1. Each experiment was repeated at least once. All exposures were initiated by the addition of appropriate amounts of copper chloride to the chambers. The continuous exposure of the test organisms continued until all animals died or, in the case of embryos, until hatching occurred or, in the case of the larvae, until yolk sac absorption occurred. The pulsed exposures were terminated by transferring exposed embryos to an exposure chamber containing control seawater.

The following measurements were taken as indices of the toxic effect of copper: cumulative mortality with time, percent hatching, and larval length at hatching. The embryos or larvae were examined within the exposure chambers at each observation period with a 7× beam dissection microscope with a 21-cm depth of field. The criterion for embryo death was the lack of heart beat or body movement. Since the embryos were attached in clusters, dead embryos were not removed until the termination of a test. Larvae that hatched from pulse exposed embryos were collected, anesthesized with a 1% quinaldine solution, and preserved in 5% Formalin[2] in seawater. Measurements of the hatched larvae were made with an ocular micrometer and all obvious deformities noted. The criterion for larval death was a failure to respond to a gentle prod with a polished glass rod. Dead larvae were removed during each observation period and preserved in 5% Formalin in seawater.

Total copper concentrations were measured two

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Experimental conditions and median lethal times for bioassays determining the sensitivity of Pacific herring embryos and larvae to copper.

Experiment	Exposure period (h)	Nominal copper concentration (μg/l)	Number of organisms exposed	Mean total copper concentrations (μg/1 ± SD)	Number of water samples	Time to median lethal level (LT_{50} ± 95% confidence interval) (h)
Embryos, continuous exposure	180 (12 h after fertilization through hatching)	Control	150	4.3 ± 1.9	3	[1]
		25	48	27.9 ± 7.4	3	[1]
		35	49	38.1 ± 9.4	3	[2]144.9 ± 8.3
		45	50	44.1 ± 11.6	3	[2]134.4 ± 5.2
		55	49	51.2 ± 9.7	3	[2]134.8 ± 3.0
		100	53	127.9 ± 34.6	2	[2]115.4 ± 2.8
		200	49	235.5 ± 47.2	2	[2]98.7 ± 2.1
Larvae, continuous exposure	300 (Hatching through yolk sac absorption)	Control	100	2.5 ± 0.8	3	[1]
		300	49	274.0 ± 24.1	4	[1,3]
		600	49	572.1 ± 31.5	4	[1,2]
		1,400	50	1,349.0 ± 247.0	4	[2]41.7 ± 7.3
		2,000	51	1,969.0 ± 148.0	2	[2]23.8 ± 1.5
		2,500	49	2,425.4 ± 89.0	2	[2]20.9 ± 2.4
		3,500	51	3,430.5 ± 710.6	2	[4]15.6
						Time to median lethality following termination of pulse ± 95% confidence interval (h)
Embryos, pulsed exposures:						
Pulse I	36 (62 through 98 h after fertilization)	Control	49	3.0 ± 0.08	2	[1]
		100	44	93.8 ± 6.3	3	[2]38.4 ± 2.0
Pulse II	38 (98 through 136 h after fertilization)	Control	93	3.9 ± 1.6	3	[1]
		100	94	111.9 ± 13.7	4	[2]53.9 ± 6.1
Pulse III	36 (136 through 172 h after fertilization)	Control	46	6.1 ± 0.7	3	[1]
		100	48	101.6 ± 29.3	3	[1]

[1]50% mortality not achieved at this concentration.
[2]Slope significantly different from control slope ($P < 0.01$) (Snedecor and Cochran 1967).
[3]Slope significantly different from control slope ($P < 0.05$) (Snedecor and Cochran 1967).
[4]Determined according to the method of Litchfield and Wilcoxon (1949).

to four times during each bioassay to determine the actual concentrations to which the organisms were exposed. Water samples were collected in acid-washed polyethylene jars and acidified to pH 2 with concentrated HCl. Total copper was analysed by the APDC-DDDC-MIBK extraction method described by Kinrade and VanLoon (1974). The copper concentration in extracted MIBK solutions was determined with a model 303 Perkin Elmer atomic absorption spectrophotometer, using an HGA-2100 graphite furnace with a deuterium background corrector.

Since the chemistry of copper in seawater is complex, more than one form of copper may be present in the bioassay water. To examine the form of the copper in the bioassay system water, out-flow samples were collected from the bioassay system before organisms were introduced to determine the particulate-bound fractions (>0.45μm), ionic fraction (bound by Chelex-100 resin (Riley and Taylor 1968)), and complexed fraction (not bound by Chelex-100 resin). The analysis scheme is summarized in Figure 2. To monitor the partitioning of copper into each of these fractions, copper-64 was equilibrated with water samples after they were withdrawn from the bioassay system. The partitioning of stable copper in the seawater of the bioassay system was indicated by the percentage of the initial activity recovered in each of the described fractions.

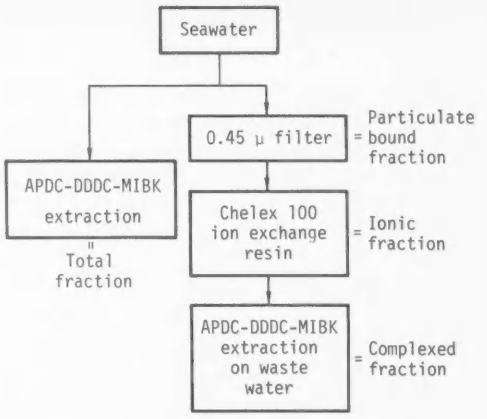

FIGURE 2.—Analysis scheme for the separation of copper fractions recovered from the bioassay system used to expose Pacific herring embryos and larvae to copper.

Statistical Analysis

The measures of toxicity determined in this study were the time to 50% mortality at each concentration of copper tested (median lethal time, LT_{50}) and the concentration of copper resulting in 50% mortality over a given time (median lethal concentration, LC_{50}). These toxicity measures were deterimed by performing a weighted linear regression analysis on the sets of cumulative mortality data using the logistic function. The straight line transform of the logistic function is: logit $P = \ln P/Q = \alpha + \beta x$, so that if logit P is plotted against x, the points will fall on a straight line with α as the intercept and β as the slope (Berkson 1953). In our calculations of LT_{50}, x represented the time from the onset of the reaction period in the case of continuous embryo exposures, from hatching in the case of continuous larval exposures, and from the termination of a given pulse in the case of pulsed embryo exposures. In our calculations of LC_{50}, x represented concentration, and our method followed that outlined by the American Public Health Association (1976) with logit analysis used in place of probit analysis.

A computer was used to calculate the LC_{50} and LT_{50} values, and for each fitted line the program determined: the LT_{50} or LC_{50}, the 95% confidence limits associated with the LT_{50} or LC_{50}, Pearson's rho (ρ), the slope (β) and the intercept (α), and the mean square error (EMS); no assumptions of homogeneity were made and the EMS was calculated in every case, rather than assuming an EMS of 1 for homogeneous data (Finney 1964).

In the case of embryos that were exposed continuously or exposed to pulses of copper, deaths prior to the delayed reaction period or the onset of the pulsed exposure, respectively, were not used in the data analysis. In no case were mortalities during these periods greater than 6%.

The relationship between time to 50% mortality during continuous exposure of both embryos and larvae and concentration was determined following the method outlined in the American Public Health Association (1976). The resulting toxicity curve was used to estimate the lethal threshold concentration (incipient LC_{50}) (Sprague 1969).

RESULTS

Physical Parameters of the Bioassay System

Mean copper concentrations measured during each test are reported in Table 1. The partitioning

of copper-64 among particulate-bound, ionic, and complexed fractions of copper recovered from the bioassay water indicates that the copper was primarily in the ionic form (Table 2). The mean pH of the water in exposure chambers in all tests was 8.08 (SD = ±0.024). The mean temperature for all tests was 13.3°C (SD = ±0.8°C).

TABLE 2.—Percentages of copper-64 in fractions of seawater recovered from the bioassay system used to expose Pacific herring embryos and larvae to copper.

Nominal copper concentration (μg/l)	Particulate bound	Ionic	Complexed	Total[1]
10	5.2	83.6	4.3	93.7
50	4.2	88.3	3.7	96.5
100	1.1	89.9	2.1	94.0
500	0.7	93.8	1.7	97.0
1,000	0.6	91.8	1.1	96.9
2,000	1.0	96.4	1.0	99.9

[1]Total includes copper-64 remaining in Chelex-100 resin after elution.

Continuous Exposures to Copper

Survival of embryos continuously exposed to copper was high at all concentrations of copper tested until 90 h of exposure, at which time dose-related mortalities occurred (Figure 3). The period during continuous exposure when embryo deaths begin is termed the reaction period. Mortalities of developing embryos at copper concentrations of 35 μg/l and higher were significantly different from controls ($P<0.01$). Virtually no hatching occurred at concentrations above 45μg/l copper. Developmental features observed in the control embryos during the onset of the reaction period included the appearance of eye pigmentation, the onset of coordinated body movements, and the initiation of heart beat. Embryos continuously exposed to copper concentrations of 100 μg/l copper and higher developed an opaque cast to the chorion, which was followed later by whitish discoloration of the body. Embryos continuously exposed to 200 μg/l copper developed an opaque change in the chorion at 60-72 h from fertilization, with body discoloration, spasmodic contractions, quiverings, and reduced fin fold development occurring at 84-96 h from fertilization.

Herring larvae continuously exposed to copper were many times less sensitive to copper than herring embryos. Larval mortalities differed significantly from controls at concentrations of 300 μg/l copper and higher ($P<0.05$) (Figure 4). Prior to death the larvae sank to the bottom of the exposure chamber and patches of whitish discoloration were observed over the bodies. Spasmodic quivering and whole body contractions were observed in larvae at concentrations of 1,400 μg/l copper and above.

The toxicity curves for continuously exposed herring embryos and larvae are shown in Figure 5. Median lethal times for each copper concentration tested and 95% confidence limits are detailed in Table 1.

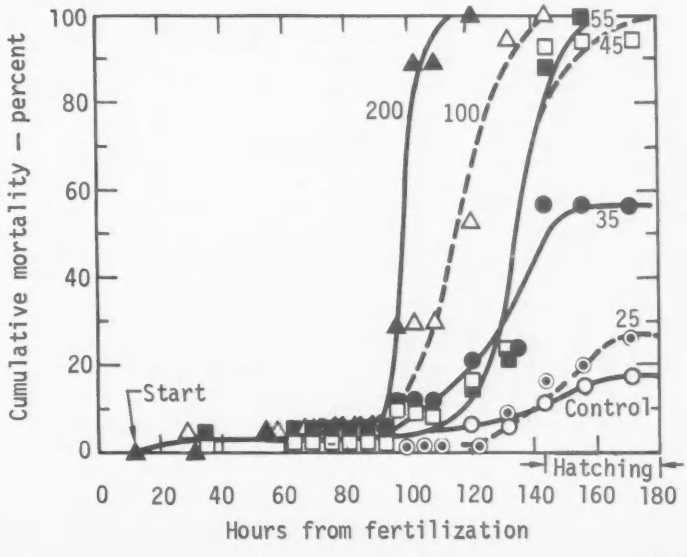

FIGURE 3.—Percent cumulative mortality of Pacific herring embryos continuously exposed to copper (micrograms per liter). Mortality curves shown are the fitted logit curves used to establish median lethal times.

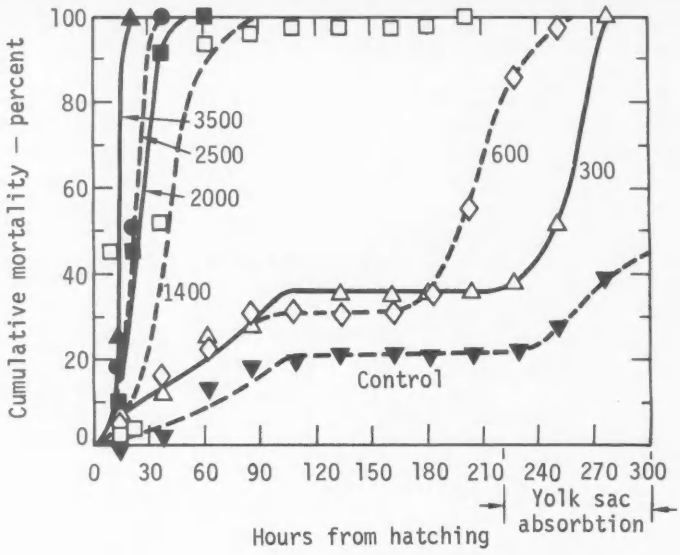

FIGURE 4.—Percent cumulative mortality of newly hatched Pacific herring larvae continuously exposed to copper (micrograms per liter). Mortality curves shown are the fitted logit curves used to establish median lethal times.

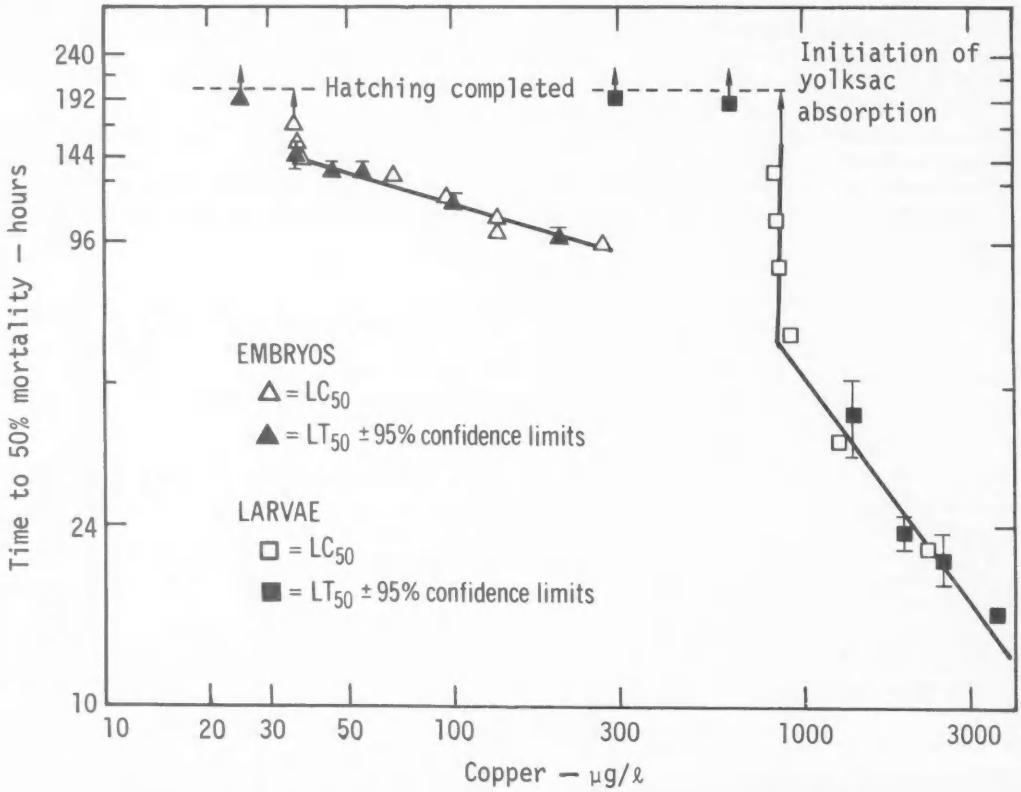

FIGURE 5.—Toxicity curves for Pacific herring embryos and larvae continuously exposed to copper.

The toxicity curve for herring embryos is presented for the purpose of discussion only, since the 90 h delay until the onset of mortality, regardless of concentration, biases the toxicity curve for comparison with other organisms without a reaction period. Sprague (1969) recommended that a concentration that killed 50% of the population during an exposure sufficiently long that acute lethal action has ceased (incipient LC_{50}) be used as the single most useful criterion for toxicity. The incipient LC_{50} is not influenced by the bias introduced by the reaction period. The estimated incipient lethal level for herring embryos was found to be 33 μg/l copper.

Only larval deaths earlier than 100 h after hatching were considered in the construction of the larval toxicity curve since larvae surviving beyond approximately 200 h after hatching have begun yolk sac absorption, and the apparently synergistic effects of copper stress and starvation can be observed in the larval time vs. percent mortality curves (Figure 4). The estimated incipient lethal level for herring larvae was found to be 900 μg/l copper.

Thirty-six Hour Pulsed Embryo Exposures

Pulses of copper exposure for 36 h showed that the sensitivity of herring embryos to copper changed as the embryos developed (Figure 6, Table 1). A 36-h pulse of 100 μg/l copper delivered during the reaction period (Pulse I) had the greatest effect upon hatching and the length of larvae at hatching (Table 3). A 36-h pulse of 100 μg/l copper delivered just before hatching (Pulse III) had a signficant effect on larval length at hatching, but the percentage of embryos hatching was actually greater than controls.

TABLE 3.—Percent Pacific herring embryos hatching and mean larval length at hatching for three groups of Pacific herring embryos exposed to 36-h pulses of 100 μg/l copper. Each group received a pulse at a different time during development.

Item	Mean larval length (mm ± SD)	Percent hatching
Controls	6.10 ± 0.47	92
Pulse 1	3.77 ± 0.2*	6
Pulse 2	4.23 ± 0.31*	47
Pulse 3	5.75 ± 0.62*	98

*Significantly different from controls ($P<0.01$) (Snedecor and Cochran 1967).

DISCUSSION

Several features of the toxic response of herring at various stages of their early life history are of interest. Previous tests examining the sensitivity of other fish embryos and larvae to copper have found that the larval stage is the more sensitive stage (Hazel and Meith 1970; McKim and Benoit 1971, O'Rear 1972; Gardner and La Roche 1973;

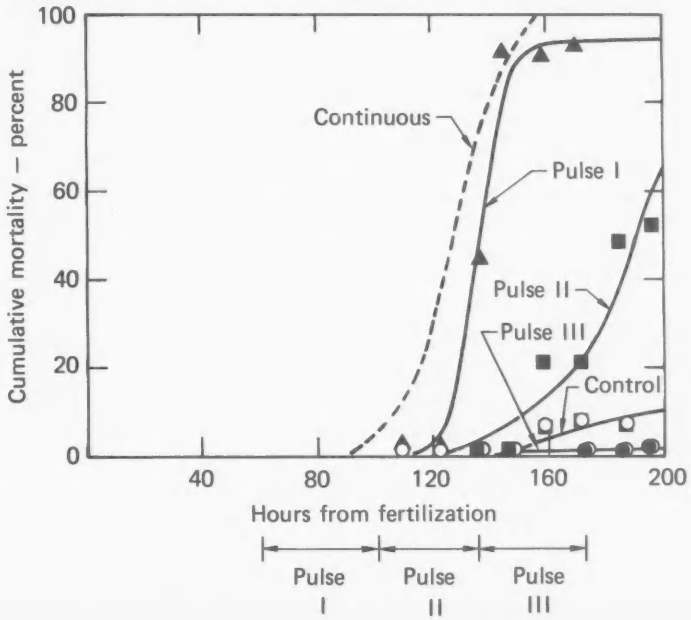

FIGURE 6.—Percent cumulative mortality of three groups of Pacific herring embryos exposed to 36-h pulses of 100 μg/l copper. Each group received a pulse at a different time during development. The cumulative mortality observed for Pacific herring embryos continuously exposed to 100 μg/l copper (See Figure 3) is shown for comparison.

Benoit 1975). Contrary to these findings, we found that embryos of the Pacific herring appear to be the stage that is more sensitive to copper. It should be noted that the fishes examined in previous studies spawn in fresh or brackish waters and cannot be considered true marine species as is the herring.

Another interesting feature of the toxic response of the herring embryos and larvae was that the behavior prior to death was similar to that of adult fish exposed to copper. Jerky, uncoordinated, and spontaneous movements were noted by Baker (1969) in the winter flounder, *Pseudopleuronectes americanus*, acutely exposed to 3,200 and 1,000 μg/l copper. Bluegill, *Lepomis macrochirus*, chronically exposed to 162 μg/l copper showed periodic involuntary spasms several weeks prior to death (Benoit 1975). The spasmodic contractions and quiverings noted in herring embryos and larvae prior to death might be of a similar nature. Baker noted that these symptoms are similar to those of Wilson's disease which also manifests spasmodic muscle contractions and quiverings in mammals. Wilson's disease is the result of an inborn error of metabolism that results in an excess of unbound copper in the blood stream (Adelstein and Vallee 1962). Goldfish, *Carassius auratus*, subjected to doses of 1,000 μg/l copper exhibit severe neurotoxic symptoms and accumulate copper in nervous tissues at levels similar to those seen in Wilson's disease (Vogel 1959).

Some of the toxic effects observed in herring embryos and larvae were similar to those reported for other heavy metals. Striped bass, *Morone saxatilis*, embryos exposed to copper or zinc (O'Rear 1972) and Baltic needlefish, *Belone belone*, exposed to cadmium (Dethlefsen et al. 1975) developed opaque discoloration of the chorion during exposure. In the present study, the chorion of the herring embryos became increasingly opaque as exposure to copper continued. Wedemyer (1968) found that in coho salmon, *Oncorhynchus kisutch*, 70% of the total zinc-65 uptake during exposure was firmly bound to the chorion, 26% was bound in the perivitelline space, and only 2% reached the yolk and 1% reached the embryo. Wedemyer (1968) also demonstrated that copper is bound by the salmon embryo's chorion. The opaque discoloration noted in herring embryos with continued exposure to copper may well be a reaction resulting from copper uptake by the chorion.

The observation of a reaction period during bioassays with herring embryos has been noted previously. A reaction period for herring embryos continuously exposed to cadmium (Rosenthal and Sperling 1974) and high temperatures and salinities (Alderdice and Velsen 1971) occurred at about the time of the onset of heart beat. The sensitivity of this developmental period in the herring was further borne out by our findings in which 36-h pulses of 100 μg/l copper during the reaction period caused higher mortalities than 36-h pulses during later developmental periods.

Pacific herring embryos may be vulnerable to toxic effects from effluents now being discharged into coastal environments. A survey of 108 municipal waste effluents on the Atlantic coast showed that 50% of the waste effluents contained >100 μg/l copper; some discharges were as high as 5,900 μg/l copper (Mytelka et al. 1973). A survey of six municipal waste discharges along the southern California coast revealed concentrations ranging from 74 to 13,900 μg/l copper with an average annual mass emission rate of 532 t of copper during 1971-74 (Mitchell and McDermott 1975). While the amount of copper discharged in the ionic form was not reported, the potential for environmental exposure levels approaching the incipient LC_{50} of 33 μg/l copper found for herring embryos in the present study should be considered in establishing water pollution control standards.

Frequently authors conducting bioassays using copper or other heavy metals have not examined the chemical state of the metal in their bioassay system. Such characterizations are important since different chemical forms of metals may have different toxic effects (Lee 1973). The method outlined in this work for examining the particulate bound fraction, the ionic fraction, and the complexed fraction of metals in seawater provides a means of examining the important chemical forms of copper in aquatic bioassay systems. With the use of appropriate isotopes this method could easily be applied to other metals. In the case of the system used to expose Pacific herring embryos and larvae it appears that the ionic form of copper predominated. In freshwater the ionic form of copper seems to be the most toxic (Pagenkopf et al. 1974). This is probably also the case for Pacific herring embryos and larvae exposed to copper in seawater.

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ESTIMATED ZOOPLANKTON PRODUCTION AND THEIR AMMONIA EXCRETION IN THE KUROSHIO AND ADJACENT SEAS

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ABSTRACT

Production and ammonia excretion of zooplankton in the Kuroshio and adjacent seas were estimated from field data of biomass, size distribution, and habitat temperature of zooplankton, and from experimental data of respiration and ammonia excretion rates as functions of body size and temperature. Winberg's basic balanced equations were applied to calculate production from respiration data. Further, mortality related to the lifespan and the ratio of herbivores to carnivores in the zooplankton community were estimated from theoretical assumptions.

In this study, 18-72% of primary production was grazed by herbivorous zooplankton, and production of herbivorous zooplankton (= secondary production) was 10-60 mg C/m² per day. The ecological efficiency between primary and secondary production was 5-22%. Ammonia-nitrogen excreted by zooplankton was 4-24 mg N/m² per day, which can support 11-44% of the nitrogen requirements of primary production.

In marine ecosystems solar energy photosynthetically fixed as organic matter by phytoplankton is channelled through zooplankton to nektonic fishes and crustaceans at higher trophic levels. Important features of the roles of zooplankton in this scheme are their extremely high conversion efficiency of phytoplankton organic matter (in contrast with terrestrial ecosystems, see Wiegert and Owen 1971; Steele 1974) and the simultaneous regeneration of nutrients through their excretory activities. The latter role is considered an important mechanism in maintaining constant primary production levels in the seas, especially in oligotrophic areas (Ketchum 1962; Corner and Davies 1971).

These dynamic functions of zooplankton have seldom been quantitatively evaluated in the field. One difficulty lies in the fact that the zooplankton community includes animals belonging to a variety of phyla and a number of species which differ geographically. Information from detailed studies on one or a few species is not adequate for this purpose, and collection of all necessary data on each component species in the community is not practical. Therefore, the development of some alternative approach is needed to overcome this problem.

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METHODS

In this study, we treat the zooplankton community as an assemblage of different sizes of animals and use body size-related constant functions for respiration and ammonia excretion from laboratory experiments to estimate feeding, production, and ammonia regeneration in the Kuroshio and adjacent seas. A systematic survey of the study area had been carried out by Japanese participants in the CSK (Co-operative Study of the Kuroshio and adjacent region) organized by UNESCO during 1965-67 (Motoda et al. 1970; Irie and Yamazi 1972).

Biomass, Habitat Temperature, and Size (= Weight) Distribution of Zooplankton

Zooplankton were sampled vertically from 150 m with a NORPAC standard net (mesh aperture, 0.35 mm) in summer (June-October 1965 and 1966) (Figure 1A) and winter seasons (December-April 1965, 1966, and 1967) (Figure 2A). From the average biomass of zooplankton summarized by Yamazi (1971) for 0-150 m, the present study area was divided into four density classes (<10, 10-50, 50-100, and >100 mg wet weight/m³). The isopleth for 100 mg wet weight/m³ shifted northward in the cold season and southward in the warm season, especially in the east China Sea (Motoda et al. 1970; Irie and Yamazi 1972). Seasonal difference in the composition of

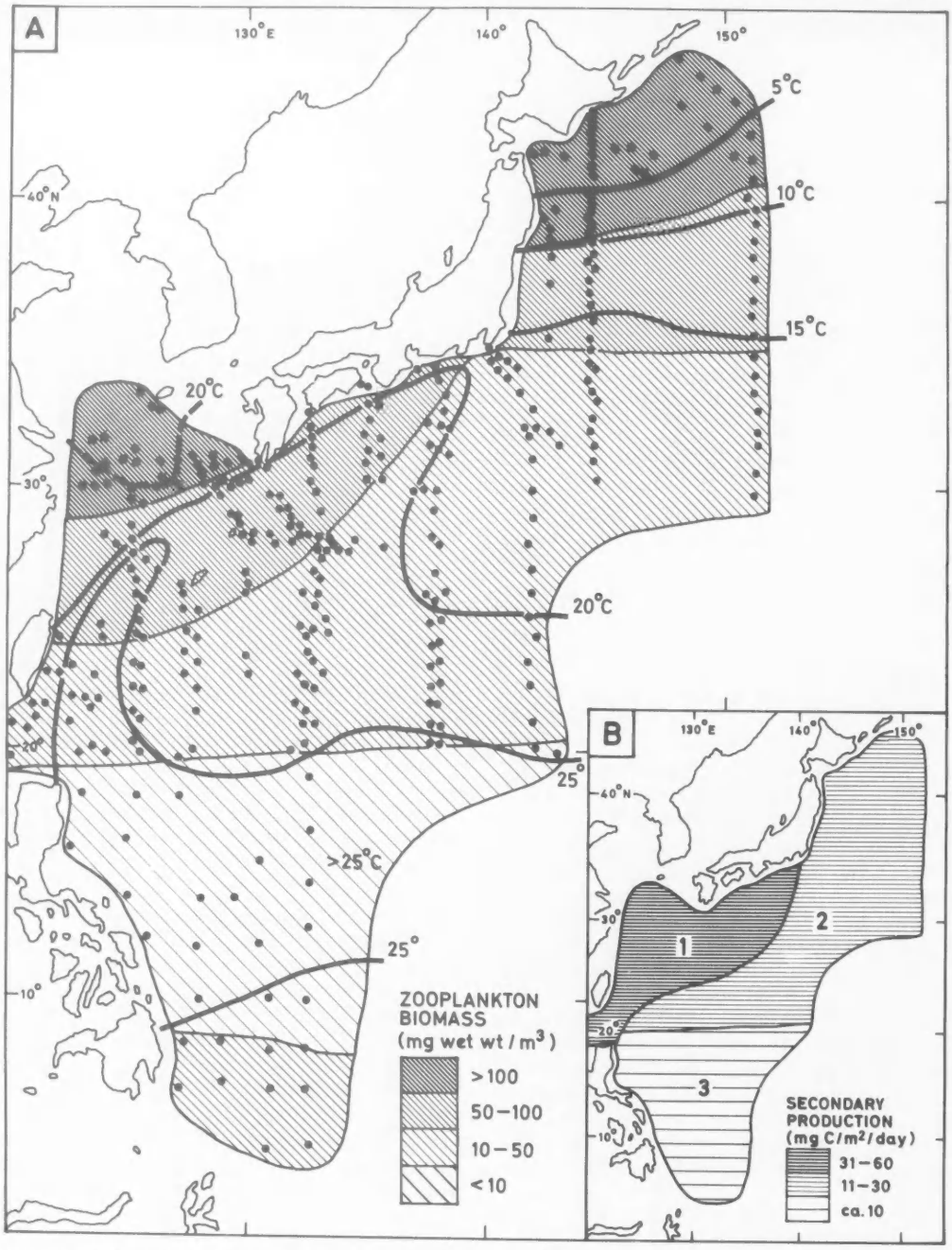

FIGURE 1.—A. Sampling stations, zooplankton biomass, and isotherms (100-m depth, continuous lines; 50-m depth, broken lines) during the warm season (June-October) in the Kuroshio and adjacent seas. B. Distribution of estimated secondary production.

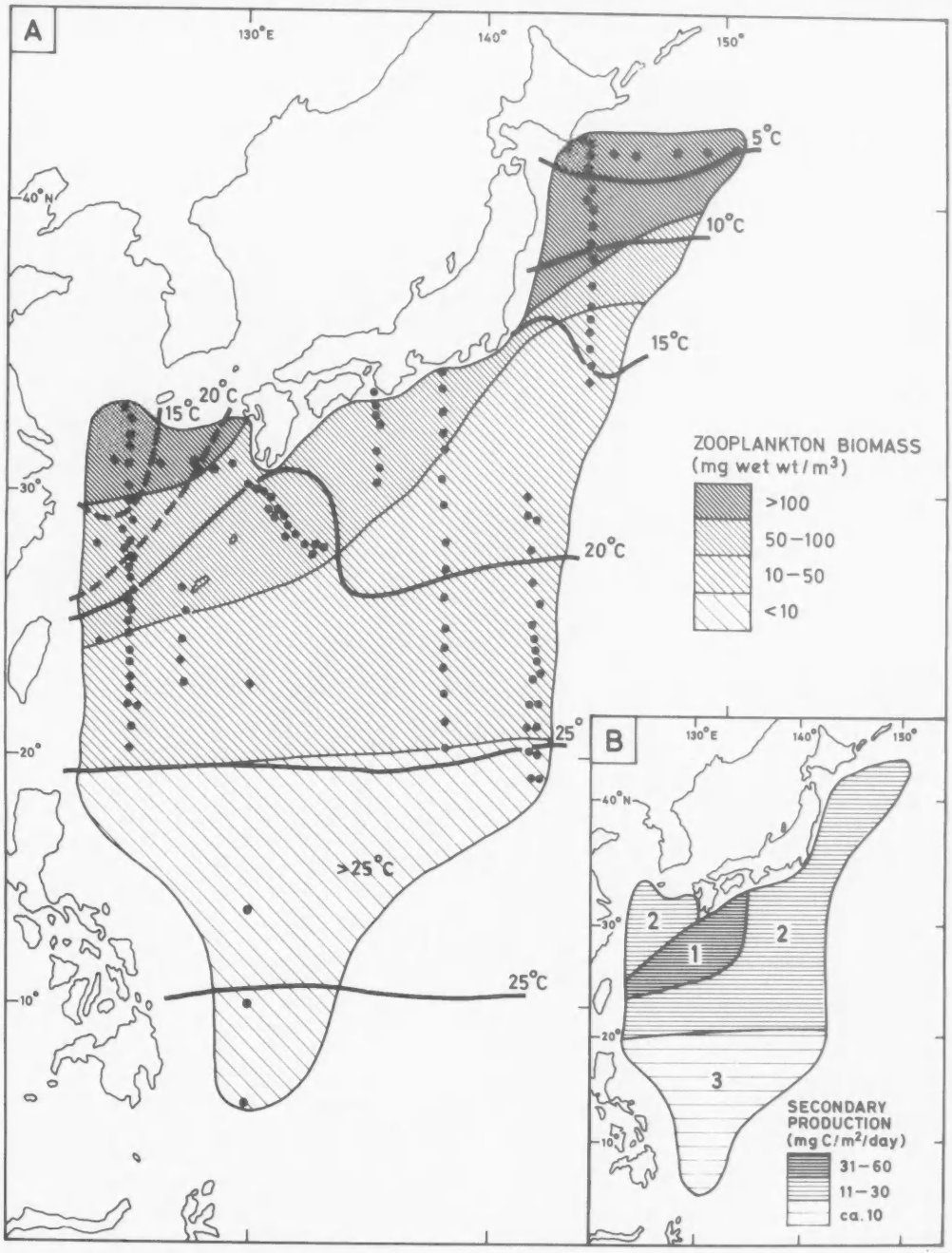

FIGURE 2.—A. Sampling stations, zooplankton biomass, and isotherms (100-m depth, continuous lines; 50-m depth, broken lines) during the cold season (December-April) in the Kuroshio and adjacent seas. B. Distribution of estimated secondary production.

zooplankton taxonomic groups among stations was less pronounced, with copepods dominant (56-65% of total individual number), followed by *Noctiluca* (8-15%), appendicularians (6-7%), and chaetognaths (4-5%) (Yamazi et al. 1972). Biomass expressed per cubic meter was converted to per square meter by multiplying by depth of sampling.

The habitat temperature of zooplankton from 0-150 m was represented by that at 100 m (Japanese Oceanographic Data Center 1967, 1969). In the east China Sea, which is shallower than 150 m, the temperature at 50 m was taken as the habitat temperature (Figures 1A, 2A).

From data summarized by Yamazi (1971), the biomass of zooplankton per haul was divided by total number of individuals per haul to obtain average body weight. Values thus obtained at all sampling stations were grouped into warm or cold season, and assumed as a general size distribution in each season (Figure 3). The highest frequency was observed in the range 0.1-0.2 mg wet weight/animal in both seasons. Faunal differences south and north of the subarctic boundary (ca. lat. 40°N) reported by Motoda and Marumo (1965) were ignored here, because no systematic difference was found in average body size of zooplankton between these areas. The skewed size distribution was converted to a normal distribution curve by logarithmic transformation (base 10). Fitness to the curve was tested primarily by the normal probability paper (Harding 1949) and finally confirmed by chi-square test (warm season: $\chi^2 = 17.85$, df = 6, $P<0.01$; cold season: $\chi^2 = 7.24$, df = 6, $0.25<P<0.5$). The normal distribution curves of log body size thus obtained were $\mu = -0.8033$ (SD = 0.2856) for the warm season and $\mu = -0.7350$ (SD = 0.3705) for the cold season.

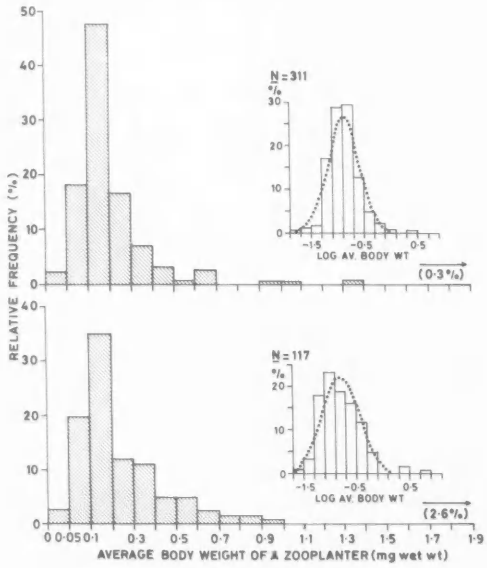

FIGURE 3.—Relative frequency of average size of zooplankton (biomass/number of zooplankton at each sampling station) in warm (June-October) (upper figure) and cold (December-April) (lower figure) seasons in the Kuroshio and adjacent seas. A normalized frequency distribution fitted by logarithmic transformation of body weights is superimposed on the right side of each figure. N is number of sampling stations.

Respiration and Ammonia Excretion

From measurements of respiration and ammonia excretion rates on various zooplankton species from tropical to boreal seas, Ikeda (1974) found that the body weight and habitat temperature are most important factors which affect rates. As a result of stepwise regression analyses, the relationship among these parameters was expressed as:

$$R \text{ or } E = aW^b \quad (1)$$

$$\text{or } \log_{10}R \text{ or } \log_{10}E = \log_{10}a + b \log_{10}W \quad (2)$$

where R is respiration rate (μl O_2/animal per h); E, ammonia excretion rate (μg N/animal per h); and W, body dry weight (mg/animal). Constants, a and b, are given as a function of habitat temperature (°C) (Ikeda 1974 amended the bias introduced by logarithmic transformation),

$$\begin{aligned} \text{for } R\text{:}\quad b &= -0.01089T + 0.8918 \\ \log_{10} a &= 0.02538T - 0.1259 \\ \text{for } E\text{:}\quad b &= -0.00941T + 0.8338 \\ \log_{10} a &= 0.02865T - 1.2802. \end{aligned}$$

Combining the normalized body size distribution of zooplankton obtained above and the values in Table 1, total respiration and ammonia excretion rates were estimated from the sum of the rates of six classes of the normal distribution curve equally divided by the SD, i.e., −3 to −2, −2 to −1, −1 to 0, 0 to 1, 1 to 2, and 2 to 3, which covers over 99% of the total area under the curve. In each class, body size of zooplankton was represented by the median value, i.e., SD = −2.5, −1.5, −0.5, 0.5,

TABLE 1.—Analysis of body size distribution of zooplankton in the Kuroshio and adjacent seas from a normalized catch distribution curve. Warm season (June-October): $\mu = -0.8033$, SD = 0.2856; cold season (December-April): $\mu = -0.7350$, SD = 0.3705. The interval of $\mu \pm 3$ SD of the normal curve was equally divided by the SD class intervals (1-6), and median value in each class interval was taken as the representative body size ($W_1 - W_6$) for that class interval.

Class interval		Median body size		Median body size equivalent (mg wet wt/animal)		Theoretical frequency (%)
No.	SD	Wt	SD	Warm	Cold	f
1	−3 to −2	W_1	−2.5	0.030	0.020	2.15
2	−2 to −1	W_2	−1.5	0.058	0.051	13.59
3	−1 to 0	W_3	−0.5	0.113	0.120	34.13
4	0 to 1	W_4	0.5	0.218	0.282	34.13
5	1 to 2	W_5	1.5	0.422	0.662	13.59
6	2 to 3	W_6	2.5	0.815	1.553	2.15
				ΣWf = 19.63	26.79	Σf = 99.74

TABLE 2.—Respiration and ammonia excretion rates per unit biomass of zooplankton in warm (June-October) and cold (December-April) seasons as derived from calculations in the text.

Habitat temp (°C)	Respiration rate (μg C/mg dry wt per h)		Ammonia excretion rate (μg N/mg dry wt per h)	
	Warm	Cold	Warm	Cold
5	0.790	0.735	0.162	0.148
10	1.300	1.183	0.270	0.242
15	2.144	1.911	0.450	0.396
20	3.538	3.091	0.750	0.648
25	5.849	5.011	1.252	1.065

1.5, and 2.5. Then, total respiration (R_{tot}) and total ammonia excretion rates (E_{tot}) became

$$R_{tot} = R_1 f_1 + R_2 f_2 + \ldots + R_6 f_6 \quad (3)$$

$$E_{tot} = E_1 f_1 + E_2 f_2 + \ldots + E_6 f_6 \quad (4)$$

where $R_1, R_2, \ldots, R_6$ and $E_1, E_2, \ldots, E_6$ are the respiration rates and ammonia excretion rates of zooplankton with body weight $W_1, W_2, \ldots, W_6$, respectively, and $f_1, f_2, \ldots, f_6$ are respective theoretical frequencies (= individual number) in each weight category. A wet weight:dry weight conversion factor of 10 was assumed (Wiebe et al. 1975). Frequency $f_1, f_2, \ldots, f_6$ of a given zooplankton biomass (ΣW) was calculated by multiplying $f/\Sigma Wf$. To facilitate calculation, respiration and ammonia excretion rates per unit biomass of zooplankton characterized by the size distribution curve in warm and cold seasons were computed as functions of habitat temperature (Table 2). Respiration was expressed as carbon units assuming $RQ = 0.8$ (protein metabolism).

Feeding and Production Estimates From Respiration

Winberg (1956) proposed the following basic balanced equations for fishes:

$$0.8F = P + R \quad (5)$$

$$K_1 = P/F \cdot 100 \quad (6)$$

$$K_2 = P/(0.8F) \cdot 100 \quad (7)$$

where F is feeding; P, growth (= production); R, respiration; K_1, gross growth efficiency; K_2, net growth efficiency; and 0.8, digestion efficiency for fishes. From these equations F and P are derived by knowing R and K_1,

$$F = 100R/[0.8(100 - K_2)] = 100R/(80 - K_1) \quad (8)$$

$$P = K_2R/(100 - K_2) = K_1R/(80 - K_1). \quad (9)$$

Apparently both digestion efficiency and gross growth efficiency (K_1) of marine zooplankton differ to a great degree, not only among zooplankton species but also within a single species (Table 3). Marshall and Orr (1955a) observed that the digestion efficiency of *Calanus finmarchicus* changed with a variety of food phytoplankton species offered. Apparently K_1 can be affected by developmental stages (Mullin and Brooks 1970b; Paffenhöfer 1976; Harris and Paffenhöfer 1976), feeding rate (Mullin and Brooks 1970b; Harris and Paffenhöfer 1976), kinds of food (Paffenhöfer 1976), and method of estimation (Butler et al. 1969, 1970). Moreover, both quality and quantity of foods used in these experiments are not necessarily the same as those that zooplankton will meet in the field. Although we have little information about the exact nature of foods of zooplankton in the field, their digestion efficiency is assumed to be quite high, because zooplankton have an ability to select suitable foods (Lasker 1966; Marshall 1973). The value of K_1 has a tendency to increase with a decrease in food concentration (Mullin and Brooks 1970a; Harris and Paffenhöfer 1976). In the field, food concentration is much lower than in laboratory experiments so that a higher K_1 value would be expected.

For these reasons we finally chose values of 70% for digestion and 30% for K_1 as realistic values of zooplankton in the field, regardless of species and food habit. Then, Equations (8) and (9) for fishes were rewritten for zooplankton, as

$$F = 100R/(70 - 30) = 2.5R \quad (10)$$

TABLE 3.—Digestion efficiency and gross growth efficiency (K_1) of marine zooplankton species obtained from laboratory experiments. Methods of estimation are with radioactive isotopes (^{14}C, ^{32}P, and ^{35}S), elemental analyses (C, N, and P), calories, weight, and ratio method of Conover (1966a). (Means in parentheses.)

Zooplankton species	Digestion efficiency and method of estimation		K_1 and method of estimation		Sources
Calanus finmarchicus	26-99	^{32}P			Marshall and Orr (1955a)
Calanus finmarchicus	53-78	^{14}C			Marshall and Orr (1955b)
Euphausia pacifica			11-74(32)	^{14}C	Lasker (1960)
Calanus helgolandicus	74-91	dry wt			Corner (1961)
Temora longicornis	52-98	^{32}P			Berner (1962)
Calanus hyperboreus	44-65 (55)	ratio method	4-36(21)	weight	Conover (1964)
			5-50(30)	calories	
Calanus finmarchicus and *C. helgolandicus*			36	N	Corner et al. (1965)
Calanus hyperboreus	39-86(69)	ratio method			Conover (1966a)
Mixed zooplankton	18-92(63)	ratio method			Conover (1966a)
Calanus hyperboreus	40-87	ratio method			Conover (1966b)
Euphausia pacifica	46-95(84)	^{14}C	6-46(26)	^{14}C	Lasker (1966)
Calanus finmarchicus and *C. helgolandicus*	54-68(62)	N	14-34	N	Corner et al. (1967)
Metridia longa	54-57	ratio method			Haq (1967)
Metridia lucens	35-94(70)	ratio method			Haq (1967)
Calanus finmarchicus			21-38	N	Butler et al. (1969)
and *C. helgolandicus*			19-35	P	
Calanus finmarchicus	77	P	17	P	Butler et al. (1970)
and *C. helgolandicus*	62	N	27	N	
Calanus helgolandicus			34-35	C	Mullin and Brooks (1970a)
Rhincalanus nasutus			30-45	C	Mullin and Brooks (1970a)
Sagitta hispida			36	N	Reeve (1970)
Lucifer chasei	8-22	^{35}S	7-14	calories	Zimmerman (1973)
Chiridius armatus	81-97	ratio method			Alvarez and Matthews (1975)
Calanus helgolandicus			3.7-35	C	Paffenhöfer (1976)
Pseudocalanus elongata			14-18	C	Harris and Paffenhöfer (1976)
Temora longicornis			17-27	C	Harris and Paffenhöfer (1976)

$$P = 30R/(70 - 30) = 0.75R. \quad (11)$$

Mortality Loss During Production

Production calculated as in Equation (11) assumes zero mortality. But production is always accompanied by mortality, caused mainly through predation by other animals and natural physiological mortality. We considered only mortality from the latter source.[3]

Assuming that 1 ml of oxygen is required to combust about 1 mg of organic matter (Jörgensen 1962), the instantaneous growth rate of zooplankton is expressed as follows from Equations (1) and (11),

$$dW/dt = (0.75/1{,}000)aW^b \quad (12)$$

where W is body dry weight (milligrams) and t, time (hours). The time required to grow from egg (W_0 in milligrams) to adult (W in milligrams) is derived from the integrated form of Equation (12),

$$t = 1{,}000\,(W^{1-b} - W_0{}^{1-b})/(0.75(1 - b)). \quad (13)$$

Chiba (1956) measured egg size in 55 species of copepods. From his data and the body length-weight relation of copepods developed by Krylov (1968) the W_0:W ratio was calculated as 0.0001:1 to 0.01:1. A similar range of the ratios is also found in the data of euphausiids, reviewed by Mauchline and Fisher (1969). The lifespan of zooplankters was defined arbitrarily as $1.5t$ (duration of adult stage is one-half that of the preadult). Daily mortality (M) caused by the length of life span becomes

$$M = 24/(1.5t). \quad (14)$$

Total mortality (M_{tot}) of the zooplankton community in terms of percent of biomass is given in the following equation:

$$M_{tot} = 100(M_1f_1W_1 + M_2f_2W_2 + \ldots + M_6f_6W_6) \div (f_1W_1 + f_2W_2 + \ldots + f_6W_6) \quad (15)$$

where $M_1, M_2, \ldots, M_6$ are daily mortalities of zooplankters with body weight $W_1, W_2, \ldots, W_6$,

[3] In addition to natural physiological mortality, molting loss by copepods, the most dominant group in zooplankton community, was included in the original calculations of Ikeda and Motoda (1975). Here we ignore the molting loss because neither molting intervals nor body size at molting were known. Therefore, present production estimate (10-60 mg C/m² per day) is slightly higher than original one (9-57 mg C/m² per day; Ikeda and Motoda 1975).

TABLE 4.—Daily mortality related to the lifespan of zooplankton in warm (June-October) and cold (December-April) seasons as derived in the text.

Habitat temp (°C)	Season	Weight ratio of egg to adult			Average (% of biomass)
		0.01:1	0.001:1	0.0001:1	
5	Warm	0.68	0.53	0.46	0.51
	Cold	0.63	0.49	0.43	
10	Warm	1.24	1.01	0.91	0.96
	Cold	1.13	0.92	0.83	
15	Warm	2.27	1.92	1.77	1.81
	Cold	2.03	1.71	1.58	
20	Warm	4.14	3.60	3.39	3.37
	Cold	3.63	3.15	2.96	
25	Warm	7.51	6.69	6.40	6.21
	Cold	6.45	5.74	5.49	

respectively. For M_{tot} as a function of habitat temperature and W_0:W ratio (0.0001:1, 0.001:1, and 0.01:1) see Table 4.

Ratio of Herbivores to Carnivores in Zooplankton Community

Although zooplankton include both herbivores and carnivores, this distinction of food habits is probably of little importance regarding ammonia excretion by zooplankton. However, the difference is essential when production is considered, especially secondary production.

We assumed that the zooplankton community at any trophic level is represented by a similar size distribution, same digestion efficiency (70%) and same K_1 value (30%). Assuming that the daily production of herbivores $(0.75a\Sigma W_i^b\,(b_i/B_0)B_0)$ equals the daily consumption by the primary carnivores $(2.5a\Sigma W_i^b\,(b_i/B_1)B_1)$ (derived from Equations (1), (3), (10), and (11)) the relation can be simplified to

$$B_1 = (0.75/2.5)B_0 \qquad (16)$$

where B_0 and B_1 are the total number of herbivores and primary carnivores, respectively, in a community, and b_i is the number of zooplankters of a given body size. Assuming that the daily production of carnivores in the lower trophic level is equal to the daily feeding of carnivores at the next trophic level, the number of carnivores at trophic level n becomes

$$B_n = (0.75/2.5)^n B_0 . \qquad (17)$$

The total number of zooplankters from the primary carnivore level to the carnivore trophic level n becomes

$$B_1 + B_2 + \ldots + B_n = B_0((0.75/2.5) + (0.75/2.5)^2 + \ldots + (0.75/2.5)^n)$$
$$= B_0\,((0.75/2.5)\,(1 - (0.75/2.5)^n))/(1 - 0.75/2.5).$$

If the number of trophic levels of carnivores is simply taken as 2, then the number of primary and secondary carnivores can be calculated to be

$$B_1 + B_2 = 0.39B_0.$$

This value does not differ greatly from the value obtained when an infinite number of carnivorous trophic levels are considered

$$B_1 + B_2 + \ldots + B_\infty = 0.43B_0.$$

Therefore, the value 0.4:1 seems appropriate for the ratio of numbers of carnivorous zooplankton to all herbivorous zooplankton.

RESULTS AND DISCUSSION

Distribution of estimated production of herbivorous zooplankton (i.e., secondary production) is summarized for warm and cold seasons in Figures 1B and 2B. Table 5 summarizes our estimates for grazing, production, and natural physiological mortality of herbivorous zooplankton and ammonia-nitrogen excretion of zooplankton (herbivores plus carnivores).

Production

The present use of Winberg's balanced equations to estimate productivity (growth) from data on respiration is not new. Shushkina (1968) estimated the production of the copepod, *Haloptilus longicornis*, in the Fiji Sea from an indirectly calculated respiration rate for this species and K_2 values from the literature including zooplankton species. In order to determine whether zooplankton in the field were supplied adequate food, we used a set of values for digestion efficiency, and gross growth efficiency (K_1), instead of a single value of net growth efficiency (K_2), to obtain feeding requirements and production simultaneously (which is not possible when K_2 is used, see Equation (8)). When the feeding requirements of zooplankton exceed food availability (i.e., food shortage), any estimate of production from Winberg's equation is unrealistic. However, our data indicate that feeding requirements of herbivorous zooplankton was 18-72% of primary production (Table 5).

TABLE 5.—Estimates of grazing, production (corrected for natural physiological mortality), and ammonia nitrogen excretion of zooplankton collected from 0 to 150-m depth with NORPAC net (0.35-mm mesh) in the Kuroshio and adjacent seas, together with primary production values from the literature (Anonymous 1967, 1968, 1969; Saijo et al. 1972). For designation of subareas, see Figures 1B and 2B.

Item	Subarea 1	Subarea 2	Subarea 3	Range
Zooplankton:				
a. Herbivorous zooplankton grazing (mg C/m² per day)	107-214	36-107	ca. 36	36-214
b. Herbivorous zooplankton production (mg C/m² per day)	31-60	11-30	ca. 10	10-60
c. Herbivorous zooplankton natural physiological mortality (mg C/m² per day)	1-4	0-2	ca. 1	0-4
d. Zooplankton excretion (mg N/m² per day)	12-24	4-12	ca. 4	4-24
Phytoplankton:				
e. Primary production (mg C/m² per day)	200-500	50-500	50-200	50-500
f. Phytoplankton nitrogen requirement (mg N/m² per day)	35-88	9-88	9-35	9-88
Phytoplankton:zooplankton relation:				
g. Ratio of herbivorous zooplankton grazing to primary production (a/e) (%)	43-54	21-72	18-72	18-72
h. Ecological efficiency from primary production to secondary production (b/e) (%)	12-16	6-22	5-20	5-22
i. Ratio of zooplankton nitrogen excretion to phytoplankton nitrogen requirement (d/f) (%)	27-34	14-44	11-44	11-44

Engelmann (1969) summarized annual production (P_a) and respiration (R_a) of animal populations (mostly terrestrial invertebrates and vertebrates) and found that $\log_{10}P_a$ was proportional to $\log_{10}R_a$. His findings were further confirmed with a large amount of data by McNeill and Lawton (1970). For comparatively short-lived poikilotherms (generation time <2 yr) the relation is expressed in the following equation (McNeill and Lawton 1970),

$$\log_{10}P_a = 0.8262 \log_{10}R_a - 0.0948$$

or

$$P_a = 0.804\, R_a^{0.8262}$$

This empirical equation resembles $P = 0.75\, R$ (Equation (11)) that we derived from Winberg's equations for marine zooplankton in this study.

Mullin (1969) reviewed production estimates for marine zooplankton and gave 5-224 mg C/m² per day as a summary value for zooplankton production at various sea areas, exclusive of values on a single species. Our estimate of secondary production (10-60 mg C/m² per day) falls in these ranges. It is noted, however, that some data cited by Mullin (1969) are on mixed zooplankton (herbivores plus carnivores) so that these are not comparable to our results which referred only to herbivorous zooplankton. For the same reason, the ecological efficiency between primary production and secondary production obtained in our study (5-22%) is not necessarily comparable to the ratio of zooplankton production to primary production (9-58%) in Mullin (1969).

Ammonia Excretion

The Kuroshio and its adjacent region in the Pacific Ocean (south of the subarctic boundary at ca. lat. 40°N) are oligotrophic (Reid 1962). Taniguchi (1972) studied geographical variation of primary production in the western Pacific Ocean and suggested that nutrients are the most important factor limiting the primary production level in the Kuroshio region. In situ primary production reported in this area is in the range of 50-500 mg C/m² per day (Anonymous 1967, 1968, 1969; Saijo et al. 1972) which is equivalent to 9-88 mg N/m² per day from a C:N ratio of 5.7:1 on phytoplankton (Redfield et al. 1963). Our estimate of ammonia-nitrogen regeneration through zooplankton excretion which can support 11-44% of the nitrogen requirement for primary production was 4-24 mg N/m² per day. Eppley et al. (1973) estimated that 40-50% of nitrogen demand for primary production was supplied by zooplankton excretion in the nutrient depleted subtropical gyre of the northern Pacific Ocean. A significant contribution of zooplankton excretion (up to 77-90% of the nitrogen requirement for primary production) was reported in Long Island Sound (Harris 1959) and offshore waters off the Washington and Oregon coasts in summer (Jawed 1973). The importance of ammonia as a nitrogen source for phytoplankton is further substantiated by its preferential utilization by phytoplankton (cf. Dugdale 1976).

Future Aspects

The production and ammonia regeneration models presented here are advantageous for understanding the marine zooplankton community which includes diversified species and widely divergent body sizes, like those inhabiting subtropical and tropical seas. Models require basically

three parameters: zooplankton biomass, size distribution, and habitat temperature. Although we obtained size distribution indirectly it should be obtainable directly. The fitting of zooplankton size distribution data to the normal distribution curve may not be necessary in some instances but this will facilitate calculations. To estimate production from respiration data, constant values of digestion efficiency and K_1 were used in this study, but these can be used as variables. From morphological characteristics of feeding organs, Timonin (1971) reported that 50-80% of zooplankton biomass in the Indian Ocean were carnivores and Motoda and Minoda (1972) reported that 20-27% of zooplankton numbers in the Kuroshio region were herbivores. These values are below the herbivore:carnivore ratios we calculated.

Since only zooplankton data were collected with 0.35-mm mesh nets and smaller zooplankters pass through this mesh size, we probably underestimated zooplankton biomass. According to Beers and Stewart (1971) biomass of microzooplankton including copepod nauplii, ciliates, foraminiferans, and radiolarians was 12-71% (24% on average) of total zooplankton collected in 202-μm nets in the eastern tropical Pacific Ocean. The important role of microzooplankton as a secondary producer and nutrient regenerator in pelagic marine ecosystems is anticipated but suitable data are yet unavailable for modeling.

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GROWTH RATE OF THE SAND CRAB, *EMERITA ANALOGA*, (HIPPIDAE) IN TWO DIFFERENT ENVIRONMENTS

CRAIG FUSARO[1]

ABSTRACT

The field growth rate of *Emerita analoga* was estimated under two different sets of environmental conditions. One beach location on the southern California coastline near Santa Barbara was compared with a beach on Santa Cruz Island, only 42 km distant. The island population of *E. analoga* experienced colder water which contained less suspended solids than the mainland population studied. The crabs on the island beach were found to grow at about one-third the rate of those on the mainland, as measured by the "instantaneous growth rate" technique.

The growth rate of a crustacean species is of considerable ecological interest for at least two reasons. First, the usual positive relationship between body size and fecundity means that an increased growth rate may increase reproductive output. Second, the proportion of animals which are mature within any specified population will depend on the growth rate (to maturity) of its members. These relationships indicate that a measure of individual growth, averaged for a population, may give information about reproductive success and, therefore, about the persistence of a population under its particular set of environmental circumstances. Further, comparison of the growth rates for populations of the same species under differing environmental regimes may indicate how the species responds to its environmental conditions in terms of growth.

The proximity of the Channel Islands to the mainland near Santa Barbara provides excellent opportunity for comparative studies. The differing oceanographic conditions between some beaches of Santa Cruz Island and nearby Goleta Bay on the mainland allow an analysis of growth as a function of different environmental characteristics. This is the intent of the present work.

This study is an analysis of the growth rate in two nearby populations of the sand crab, *Emerita analoga*. It is an anomuran crab which inhabits beaches of the eastern North Pacific from southern Canada to central Baja California. There also are populations of the species in the Gulf of California and the eastern South Pacific, but these populations are not considered here. The crab normally lives between high and low tide marks buried in sand on sandy beaches, and follows the water's edge up and down the beach with the tides. The crab is somewhat unusual for its family in that it procures its food by filtering seawater that washes over its finely setose second antennae as waves rush onto and ebb from the beach face. *Emerita analoga* can often be found in dense aggregations on beaches of southern California during spring and summer. This species was chosen for comparative growth study because: 1) it is seasonally very abundant and easily captured in great numbers; 2) it is of a size which facilitates the handling and treatment of such numbers; and 3) it inhabits beaches of the mainland and beaches on nearby Santa Cruz Island.

Several methods have been used in the past to measure the incremental type of growth experienced by crustaceans, all of which have merits and drawbacks. These methods include: field caging, laboratory confinement, mark and recapture methods, and modal size class analysis. The best of these for the estimation of field growth rate is field caging. This method, unfortunately, cannot be applied to sand crabs living in their shifting sand habitat. For reasons presented in detail in the methods, a different approach has been used to measure growth for *E. analoga* The "instantaneous growth rate" method used here takes advantage of certain aspects of the crustacean molt cycle to minimize handling effects while estimating field growth rate. Both molt increment and molt frequency measures are taken, which are combined to give an instantaneous growth rate for an average individual of each population. By this method the response of growth to different en-

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vironmental conditions in the field can be observed for this species.

METHODS

Several alternatives for the measurement of growth for *Emerita analoga* were possible, including all those mentioned above. Field caging did not seem practical, and laboratory impoundment does not provide information on the growth rate in the field situation. Mark and recapture techniques are adaptable to the species (Dillery and Knapp 1970), but considerable time and effort can be expended for very little data return. The usual recapture rate is low, 10% or so at best, unless unusual circumstances, e.g., a fishery, exist. Modal size class analysis can give an index of average growth, but can be misleading without corroborative evidence from the laboratory or some other method of growth measurement. Unfortunately, no such corroborative data exist for *E. analoga*. As a result of these considerations, an instantaneous growth rate method was chosen to estimate growth for this species. This method as applied to *E. analoga* is described in the following sections.

Localities

Two locations were chosen on the basis of their proximity and on preliminary observed differences in their environmental conditions. One site, the beach of Goleta Bay adjacent to the University of California Santa Barbara campus, is bathed in relatively warm water (mean surface temperature for 1974 and 1975: 13.7°C) that is relatively turbid (average lateral visibility: <1 m).

The second site, a bay on the northwest corner of Santa Cruz Island, is about 42 km (25 mi) south of the coast of Santa Barbara, and experiences much different water conditions. At this location, water clarity is almost always excellent (10-20 m of lateral visibility), indicating a relative lack of suspended materials. In addition, Neushul et al. (1967) described current patterns in the vicinity which indicate that this site is bathed in a colder water mass originating in the north. The mean surface temperature measured at the Santa Cruz Island site during 1974 and 1975 was 12.1°C.

Sampling

Sand crabs were gathered and separated into size classes by methods described fully in Wenner et al. (1974). The use of an automatic size sorting sieve permitted measurement of a large number of live crabs rapidly. Samples were taken approximately biweekly at Santa Cruz Island and Goleta in 1974 and monthly at Goleta in 1975. The crabs, separated into size classes, were then placed in screen compartments in sand in a continuous flow seawater table for a period of 5 days. Every day each compartment was checked for molts, and the number of molts and molt increments were recorded. Where multiple molts occurred in any size class on 1 day, premolt and postmolt carapace length were paired by rank from least to greatest measure. This procedure might tend to reduce the variance in molt increment slightly, but no significant differences were found between single molt and multiple molt records for 20 molt increment observations during May-July at Goleta in 1974 ($0.5<P<0.6$, $t = 0.667$, df = 36).

Water temperature data were taken at the time of sampling, and water temperature was monitored throughout the 5-day holding period. Water samples were also taken monthly from July to October 1975. The water was filtered through preashed, preweighed Whatman[2] GF-C glass fiber filter paper under 4-5 lb vacuum, after coarse filtration through a 2-mm screen. Efford (1966) suggested that *E. analoga* can handle particles between 5 μm and 2 mm. The filter paper filtered particles down to approximately 5 μm in size. Thus an approximation of the range of particle sizes utilized by *E. analoga* was filtered from the water. Filterable solids (grams/liter) were measured in this way from both sites.

Instantaneous Growth Rate Rationale

Given that two parameters of crustacean growth, i.e., molt increment and molt frequency, are the factors which need be estimated, a method is required which minimizes handling effects but which still allows observation of size-specific changes in these measures.

Prolonged impoundment in a laboratory situation tends to affect both the molt increment and molt frequency; however, aspects of the crustacean molt cycle provide an advantage if crabs are held in the laboratory for a short period of time. Drach (1939) described the molt cycle of *Cancer*

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

pagurus. From this description it is clear that a crustacean actually spends a great deal of its time involved with the molting process. Once the specific stimulus to molt has occurred, environmental changes seem to have little effect in modifying the process (Green and Neff 1972). In other words, a crab which is about to molt will molt. In fact, keeping *E. analoga* in running seawater tables for a very short portion of their molt cycle does not alter a relatively high value for molt frequency and increment. For example, Table 1 shows data from a 14-day period in which *E. analoga* were kept in running seawater tables. These data suggest that for a period of 5 days or so *E. analoga* may be relatively unaffected by impoundment in running seawater tables, but that confinement for longer periods reduces both the increment at molt and molt frequency.

From the above, it follows that keeping *E. analoga* in running ambient seawater tables for a period of 5 days generates relatively accurate "instantaneous" estimates of field growth rate for these crabs. This allowed me to collect sand crabs from the field, place them in seawater tables within 2 or 3 h after collection, and monitor them daily. Molt increment was measured directly as animals within each size class molted, and molt frequency was calculated by the formula: $f_m = t/p_t$ where f_m = molt frequency in days, t = total number of days held, and p_t = proportion of animals which molted in t days. For instance, if half the crabs molted in 5 days, the average molt frequency would be 10 days.

TABLE 1.—Molt records for *Emerita analoga* kept in running seawater tables for 14 consecutive days.

Day	Total no. molts from 264 crabs	$\bar{x}$ molt increment[1]	Day	Total no. molts from 264 crabs	$\bar{x}$ molt increment[1]
1	13	1.2	8	4	0.8
2	11	1.3	9	8	0.9
3	19	1.2	10	6	—
4	27	1.0	11	5	—
5	17	1.2	12	2	—
6	9	0.8	13	3	—
7	7	0.9	14	2	—

[1]At 5.9 mm premolt carapace length.

RESULTS

Environmental Differences

Water temperature showed a consistent annual difference between Goleta Bay and Santa Cruz Island for 1974 and 1975 (Figure 1), though the peak water temperature for 1975 was the same for both locations. During June-October 1974, the mean surface temperature difference between sites was 2.9°C. Peak water temperature was maintained for about 2 mo (mid-June to mid-August) at Goleta Bay in 1974 while Santa Cruz Island experienced peak temperature for a month or less.

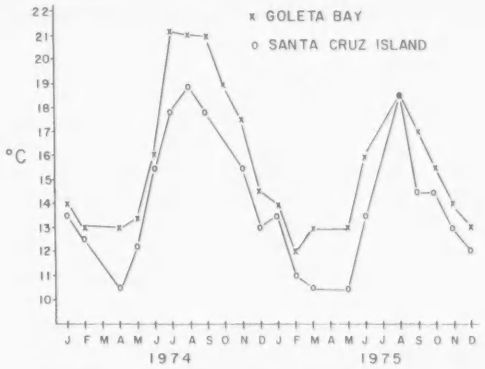

FIGURE 1.—Annual surface temperature variation at Goleta Bay and the western tip of Santa Cruz Island for several years. Data from March to October 1974 are from direct observation. All other data are from U.S. Coast Guard sea surface isotherm charts for Point Conception south.

Four water samples, taken at each location monthly between July and October 1975, showed a large significant difference ($P<0.001$, $t = 6.36$, df = 14) between the amount of filterable solids in the water washing onto the two beaches. Goleta Bay averaged 0.11321 ± 0.02933 g/l of filterable solids while Santa Cruz Island averaged 0.04416 ± 0.00925 g/l. This means that about 2½ times as much filterable material was potentially available for *E. analoga* at Goleta Bay as at Santa Cruz Island. Unfortunately, organic content of these samples was not measured. This would have been a more reliable index of food availability than filterable solids.

Growth

Comparison of data from Goleta Bay in 1974 and 1975 indicates that the instantaneous growth rate method produces repeatable results and that the growth rates at Goleta Bay for the two time periods were about the same (Table 2). Comparison of data from Goleta Bay and Santa Cruz Island in 1974 indicates that sand crabs from the island site were molting about half as often, on the average, as those crabs from Goleta Bay during the

TABLE 2.—Summarized growth data for sand crabs from Goleta Bay and Santa Cruz Island in 1974 and 1975. Mean ± SD is given for each measure.

Item	Goleta Bay		Santa Cruz Island, 1974		
	1974	1975	All samples	First 3	Last 3
Molt increment (mm):					
Sample size	581	629	188	118	70
$\bar{x}$ increment	0.9 ± 0.3	1.0 ± 0.4	0.6 ± 0.3	0.8 ± 0.3	0.4 ± 0.2
$\bar{x}$ premolt carapace length	7.3 ± 1.8	7.4 ± 4.2	7.5 ± 2.7	8.0 ± 3.0	7.4 ± 1.8
Molt frequency (days):					
Sample size	1,785	1,334	1,703	717	986
$\bar{x}$ frequency	26 ± 19	18 ± 11	50 ± 24	36 ± 18	63 ± 22
$\bar{x}$ premolt carapace length	7.7 ± 1.8	7.0 ± 3.4	7.7 ± 3.1	8.8 ± 3.5	7.0 ± 1.6

sampling period. Also, the island site crabs gained about a third less in carapace length at each molt than the mainland animals (Table 2). Thus, sand crabs at the island beach would take about three times as long as the Goleta Bay crabs to reach a given size, growing at the observed rates. Calculation of the instantaneous rate of growth (molt increment ÷ intermolt period) for the two beaches in 1974 gives values of 0.035 mm/day for Goleta Bay and 0.012 mm/day for Santa Cruz Island

Separation of the Santa Cruz Island samples into two equal time periods (May-early July, late July-September) yielded an interesting observation. The later group of samples showed a much lower growth rate than did the earlier, which can be explained by the steady decline in molt increment (Figure 2). The relatively high value (0.9 mm) in late May could represent a peak, but the island site was not sampled prior to May. The pattern of molt increment vs. time for Goleta Bay (Figure 2) was different, showing peaks in July and September. The decrease in August may reflect changes in the number of maximum size males, which decrease in molt increment as they approach maximum size, and also may reflect an influx of juvenile crabs into the population in August. The first peak corresponds in time with the peak water temperature for the sample period (Figure 1). This may be a result of a physiological response to temperature by *E. analoga*. Crabs observed in the laboratory at different temperatures fed at different rates. Those in warmer water fed most often (Fusaro 1977).

At both locations, molt increment was positively correlated with size (Figure 3). The difference between means of molt increment from the two locations was 0.3 mm, amounting to about one-half of an average molt increment for the Santa Cruz Island beach population.

Molt frequency data could not be correlated with carapace length at either location, although a generally similar trend existed in most samples. A

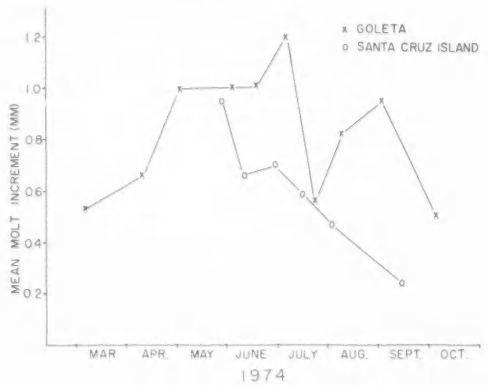

FIGURE 2.—Molt increment vs. time for sand crabs from Goleta Bay and Santa Cruz Island. Each point is a mean for that sample date.

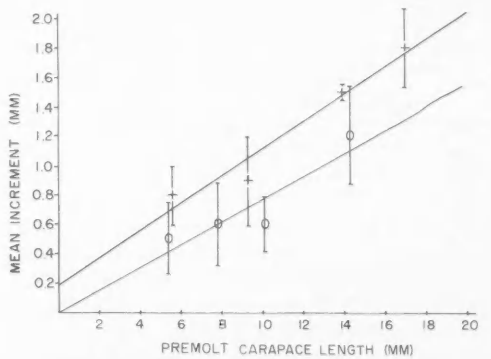

FIGURE 3.—Regression of mean molt increment on premolt carapace length for grouped size class data of sand crabs from Goleta Bay (+'s) and from Santa Cruz Island (0's). Regression line equations are $Y = 0.0932X + 0.1829$ for Goleta Bay and $Y = 0.0776X - 0.0041$ for Santa Cruz Island. Correlation coefficients are 0.98 for Goleta Bay and 0.92 for Santa Cruz Island. Vertical bars at each point represent ± 1 SD.

relatively high molt frequency was observed at smaller sizes (about every 7-12 days/molt at 5 mm carapace length), and this value increased generally in larger size classes (to about every 80-90 days/molt at 20 mm carapace length). Molt frequency averaged over a similar range of premolt carapace lengths did reveal, however, a large difference between the populations on the two different beaches (Table 2).

Population structure data reveal differences in several measures which relate to the growth rate of *E. analoga* (Table 3). The mean size of both males and females was reduced at the Santa Cruz Island site. The proportion of females larger than the mean minimum size of ovigerous females was drastically reduced at the Santa Cruz Island site (2.7% compared with 21.1% at Goleta). In addition, the overall proportion of females which were ovigerous was much smaller at the island site (1.1% compared with 19.4% at Goleta).

TABLE 3.—Population structure data from pooled samples of *Emerita analoga* between June and September 1974. All size values are in millimeters carapace length and sample sizes are in parentheses.

Item	Goleta Bay	Santa Cruz Island
Mean size ♂	7.5 (8,956)	6.0 (6,951)
Mean size ♀	9.7 (6,347)	7.5 (7,730)
Mean % ovigerous ♀	19.4 (6,347)	1.1 (7,730)
Mean min size ovigerous ♀	13.8 (6,347)	13.8 (7,730)
% ♀ >13.8 mm carapace length	21.1 (6,347)	2.7 (7,730)

DISCUSSION

Methods for Measuring Growth

The growth rate of crustaceans in nature, though of considerable research interest, has been difficult to measure for several reasons. Primarily, all of the hard parts of the animal are cast off with the molt, making the marking of them all but impossible until recent years. Wenner et al. (1974) discussed the problems associated with measuring growth for crustaceans, and their table 1 summarized possible patterns of growth for the Crustacea. That table stressed the relative contribution of two factors in crustacean growth: molt increment and molt frequency. Both of these may be responsive to different environmental parameters, altering the growth pattern of a species.

The standard methods for measuring field growth rate for crustaceans (caging, mark and recapture, and analysis of modal size classes without corroborative data) are unsatisfactory to compare field growth rates for different populations of *E. analoga*. Since none of these methods alone suffices for this kind of comparative measurement with *E. analoga*, the instantaneous growth rate approach was used in this comparative analysis. The method has qualities common to some of the other methods mentioned, but avoids some of the inherent problems of those methods. This technique allows direct observation of size-specific molt frequency and molt increment, while minimizing the handling effects normally associated with laboratory impoundment. It is likely that molt frequency estimates by this method are more accurate for the larger crabs, for which the 5-day holding period is a relatively smaller proportion of the intermolt period. The method has allowed comparison of growth factors (molt increment and frequency) in detail for *E. analoga* and gave repeatable data such as that found for Goleta Bay in 1974 and 1975. Thus a technique for measurement of crustacean growth has been developed here which may hold promise for such comparative studies as this, where field caging is impractical.

Growth of *Emerita analoga*

The large difference in the growth rate of *E. analoga* between beaches of Goleta Bay and a Santa Cruz Island bay is remarkable in view of their proximity (about 42 km apart) but not in view of the different environmental conditions found at each beach. The combination of colder water and reduced filterable material in suspension in the water appears to have slowed the growth of *E. analoga* on Santa Cruz Island. This difference is evidence of the sensitivity of these two factors of sand crab growth to variation in environmental qualities.

It is tempting to construct growth curves from such data on molt increment and molt frequency, having arrived at estimates for these. Both of these factors, however, have been shown to be highly responsive to environmental conditions. In fact, they vary widely in time and space with no clear pattern emerging as yet. A growth curve constructed from these data would apply only under a specific set of environmental conditions. Certainly these large differences in growth rate in nearby beaches precludes the use of modal size classes from several beaches for the determination of growth for *E. analoga*, as Efford (1967) did earlier.

Efford (1967:84, figure 3) presented a growth curve for *E. analoga*, constructed from data taken from 22 beaches on the Pacific coast between Ensenada, Mexico, and Tofino, Canada (a 2,400 km distance). Three-fourths of the data presented were gathered over a period of only 2 mo (between 17 June and 17 August 1961). The remaining data were collected in 1959 and 1963. Where size-frequency data were bimodal, the author assumed that two year classes were present. To construct a growth curve from his data, Efford also had to assume that: 1) growth rate was the same year to year (temporally stable, at least during the growing season); and 2) longshore migration did not take place for *E. analoga*.

Dillery and Knapp (1970) demonstrated that an average *E. analoga* individual of about 26 mm carapace length travels about 15 m/day alongshore in an easterly direction on local beaches in Santa Barbara. This implies that the individuals in inhabiting a particular location may change from day to day. Barnes and Wenner (1968) suggested that the interpretation of size-frequency data is considerably simplified if sex reversal is assumed for this species, and some direct evidence (Wenner 1972) supports this assumption. However, recent laboratory data (Fusaro 1977) suggest that a differential growth rate for males and females between 9 and 14 mm carapace length may account for the observed size-frequency distributions and sex ratio patterns, rather than protrandry.

Combining data from different beaches, as Efford (1967) did, also carries with it the assumption that the growth rate is relatively the same for the various parts of the range of *E. analoga* (spatially stable). However, in an analysis of *E. talpoida* data presented by Wharton (1942), Efford suggested that the growth pattern of this latter species may differ in the southern part of its range. It is likely that temperature was responsible for the difference, as it is likely that temperature has an effect on the growth of *E. analoga* in different parts of its Pacific coast range.

Wenner et al. (1974) presented data (their figure 5) which suggested that for *E. analoga*, even different local populations may display different growth patterns, at least as indicated by size at sexual maturity. Data presented in this report imply that molt increment and molt frequency are indeed different in different environmental regimes in nature. Growth curves constructed for such different areas would likely differ. To combine these sets of data would be to obscure the real differences in growth rate observable in such local, proximate populations.

The instantaneous growth rate estimate, though, may be used as an index of how well a population fares under a given set of environmental conditions. Consider this instance. It has been shown that a population of *E. analoga* on a beach at Santa Cruz Island grew about one-third as fast as a population in Goleta Bay (molt increment depressed by one-third and molt frequency depressed by one-half). Assuming a fixed number of molts to maturity (e.g., Wenner et al. 1974, table 1), the island population would reach maturity at a smaller size and in about twice as long a time. In fact, population structure data (Table 3) shows that sand crabs from the island population reached maturity at about the same size as those from Goleta Bay. If a fixed size at maturity is assumed, the island population sampled would take about three times as long to reach that fixed size.

The third possible assumption, that there is a fixed length of time to maturity, is argued against by all available data. In any of these cases, however, the population of sand crabs inhabiting the beach of the Santa Cruz Island bay location was at a distinct disadvantage in terms of reproductive success when compared with the population of *E. analoga* inhabiting the Goleta Bay beach. This reproductive disadvantage was brought about at least in part by the large observed differences in molt frequency and molt increment at the two locations. A much smaller percentage of females were of reproductive size, probably due to the differential growth rate (see Table 3).

Cox and Dudley (1968) also reported large variations in the size of the smallest egg bearing female *E. analoga* found in their collections. Data presented here may account for such previously problematical observations, in that differences in growth rate may affect the size distribution and abundance of mature females.

As these data suggest, then, the growth rate of a crustacean population plays an important role in the life history of that species in its particular environmental situation. Of course, when dealing with a species which has pelagic larval stages, it becomes difficult to study local populations under the assumption that they are genetically different. Recruitment patterns are not generally well known for species with pelagic larvae (see Thorson 1950; Efford 1970; Mileikovsky 1971; Strathmann

1974), thus confounding the issue of reproductive success for a population in a particular habitat. Thus "relative reproductive success" may not be as good a criterion between populations such as these as it is between species. Measurement of differences in such life history factors as growth rate may, therefore, take on added significance in the comparison of two populations or species in differing environments, inasmuch as they do not depend on the assumption of genetic isolation but concern themselves more with the relationship of the population to its particular environmental circumstances.

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TIME-DEPENDENT SOLUTIONS AND EFFICIENT PARAMETERS FOR STOCK-PRODUCTION MODELS

R. IAN FLETCHER[1]

ABSTRACT

The time-dependent formulations of the Graham-Schaefer and Pella-Tomlinson systems are restructured so as to accommodate directly the critical-point parameters of their respective governing graphs; the resulting parametric system accounts for the behavior of either model wholly in terms of its management components. The indeterminate exponent and the coefficients of the Pella-Tomlinson equations are uncoupled and the dual formulations associated with the conventional casting of the system are eliminated; the governing equations and corresponding solutions are cast into composite forms and the sign changes of coefficients become automatic. The previously obscure relationships between management parameters and variable graph curvature in the Pella-Tomlinson model are expressly formulated; maximum sustainable yield is shown to be independent of the indeterminacy of the system. Time-delay estimators for both systems are formulated.

We analyze here, in a deterministic setting, certain of the transient, nonlinear mechanisms employed in the modelling of stock and yield during periods of imbalance between fishing removals and stock productivity. The general method of analysis, which appeals primarily to the direct parameterization of critical points, will apply to any nonlinear scheme of exploitation and gross production, but it applies in particular to the Graham-Schaefer hypothesis (Graham 1935; Schaefer 1954) and to the "generalized" model of Pella and Tomlinson (1969). Since control of either system rests ultimately with the control of critical points, we restructure the parametric definitions accordingly and the governing equations for both systems are then controlled directly by parameters of management significance.

Typically, either system reflects the deterministic premise that a stock of fishes, otherwise held by exploitation at levels below a prior abundance, will constantly strive to recover its numbers in accord with some innate, self-regulating, and repeatable mechanism of restoration. Any such restoration must accrue from the productivity of the stock, and by Graham's hypothesis, the inherent or latent capacity for productivity in a stock of fishes depends jointly on the current size of the stock (in numbers or biomass) and the difference between the current and potentially maximum sizes. Whence, in terms of time-dependent biomass B, and with the proportionality coefficient defined as the ratio of "intrinsic" growth rate k and b_∞, Graham's formula for latent productivity $\dot{P}$ takes on the familiar form

$$\dot{P}(B) = kB - \frac{k}{B_\infty} B^2. \qquad (1)$$

Of the two expanded terms, the first governs the intrinsic, exponential capacity for growth of the population's biomass, while the negative, nonlinear term provides the damping that ultimately slows growth as $B(t)$ approaches its asymptotic maximum B_∞. The two terms, in their algebraic sum, govern the latent productivity of the stock at any stock size between zero and B_∞. Parameter k, as we shall see, is coupled analytically and phenomenologically to parameter B_∞, but the dependence of k on root B_∞ in Equation (1) can be supressed in favor of the direct parameterization of maximum productivity (which, in the complete exploitation model, we identify with maximum yield rate).

In the Pella-Tomlinson model, the parametric controls for latent productivity exceed by one the total number of such parameters in Graham's formulation, an increase in freedom that comes at considerable cost to tractability, both analytical and statistical. The differential equation that governs latent productivity in the Pella-Tomlinson system has the indeterminate form

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$$\dot{P}(B) = c_1 B + c_2 B^n, \tag{2}$$

with exponent n the additional parameter, but with the signs of the coefficients now dependent on the range of definition of n. As before, the combined terms describe, at any stock size B, the stock's latent capacity for productivity. With n undetermined (its determination being a part of the empirical demonstration), solutions of Equation (2) constitute infinitely many growth laws. By setting $n = 2$, and with $c_1 > 0$, $c_2 < 0$, Equation (2) reduces to the Graham equation (Equation (1)). Pella and Tomlinson (1969) attribute Equation (2) to Richards (1959). For a detailed analysis of (2) as a general growth form, see Fletcher (1975); the anticedents of this analysis appear there.

In either of the two systems, exploitation enters the formulation for productivity by the direct difference $\dot{P} - \dot{Y}$, with $\dot{Y}$ signifying the rate of biomass removal owed to exploitation and $\dot{P}$ the latent productivity of the stock. Wherefore, in writing

$$\dot{B}(B) = \dot{P}(B) - \dot{Y}(B), \tag{3}$$

we interpret $\dot{B}(B)$ as being the resultant productivity, at stock size B, that nets to the stock for its growth. The net may be positive, negative, or zero accordingly as $\dot{P}$ and $\dot{Y}$ vary with B. That is

$\dot{P} > \dot{Y}$ implies $\dot{B} > 0$: the stock's latent productivity exceeds the rate of exploitation; a positive net productivity remains to the stock and the stock so tends to a higher level of biomass.

$\dot{P} < \dot{Y}$ implies $\dot{B} < 0$: the rate of biomass removal exceeds the stock's capacity for growth; the stock adjusts to the deficit in net productivity by tending to a lower level of total biomass.

$\dot{P} = \dot{Y}$ implies $\dot{B} = 0$: the exploitation rate just balances latent productivity, and biomass trajectory $B(t)$ exhibits an extremum. Should $\dot{B} = 0$ over finite time, stock biomass remains stationary and the state called "equilibrium" prevails.

Although the detailed time course of any real stock biomass is actually determined by variations in renewal, survival, member growth, and the age- or size-dependent probabilities of capture, such effects are not usually separated in the models of interest here, and yield rate $\dot{Y}$ customarily takes the form

$$\dot{Y}(t) = F(t) \cdot B(t), \tag{4}$$

with the implication that all fish of the fishable stock are presumed to share, in equal measure, the force of fishing mortality F, irrespective of age or size. By admitting Equation (4) into Equation (3), our general form for net productivity becomes

$$\dot{B} = \dot{P} - F \cdot B, \tag{5}$$

where the time variation of F is usually prescribed by average effort f on the assumption that $F = qf/\tau$, quantity q being the individual probability of capture per unit of effort and τ the averaging interval measured in fractions of the dimensional time unit of F.

ANALYSIS OF THE GRAHAM SYSTEM

Figure 1 illustrates the phase-plane graph of Equation (1), the latent productivity of a Graham stock. Maximum productivity m occurs at stock size p. And regardless of the conventions employed in the formulation of Equation (2), essential parametric control in the equation resides specifically with its nonzero root B_∞ and with coordinate m of the critical point (p, m). Parameter m and B_∞ constitute a complete, minimum set of analytically independent parameters for latent

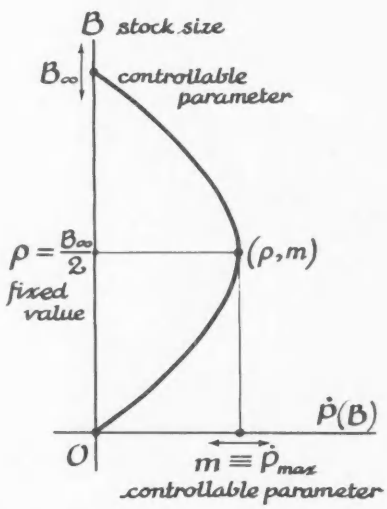


FIGURE 1.—Latent productivity $\dot{P}$ as a function of stock size B, the Graham model. See Equations (1) and (1a).

productivity in the Graham system, and they represent the whole extent of available control over the graph of Equation (1). Coordinate p of the critical point has the fixed value $B_\infty/2$, and the graph of Equation (1) has a fixed curvature of second degree.

Wherefore, productivity Equation (1), cast directly in terms of analytical parameters m and B_∞, takes on the form

$$\dot{P} = 4m\left[\frac{B}{B_\infty}\right] - 4m\left[\frac{B}{B_\infty}\right]^2, \qquad (1a)$$

and intrinsic rate k, as it turns out, bears a proportionality dependence on maximum productivity and maximum biomass in the relationship

$$k = \frac{4m}{B_\infty}\left[\equiv 4\frac{P_{\max}}{B_{\max}}\right]$$

And with the substitution of Equation (1a) into Equation (5), the formula for the net productivity of a Graham stock becomes

$$\dot{B} = 4m\left[\frac{B}{B_\infty}\right] - 4m\left[\frac{B}{B_\infty}\right]^2 - FB. \qquad (6)$$

In the integrated, equilibrium versions of the Graham system, maximum latent productivity m becomes maximum sustainable yield (MSY), hence parameter m may be directly interpreted as MSY in any optimization procedure on Equation (6).

If we restrict the time-dependence of F to abrupt changes so that any solution of Equation (6) corresponds on its interval of validity, however brief, to some constant value of F, then the time-dependence of B in Equation (6) becomes

$$B(t) = \frac{B_*}{1 + C_0 e^{-(4m/B_\infty - F)t}}$$
$$B_* = \left[1 - \frac{FB_\infty}{4m}\right] B_\infty, \qquad (7)$$

and with initial time t_0 set arbitrarily to zero, the integration constant in Equation (7) becomes

$$C_0 = \frac{B_* - B_0}{B_0}.$$

Figure 2 illustrates the relationship between net productivity (Equation (6)) and the biomass solution (Equation (7)) for cases where

$$F < \frac{4m}{B_\infty}.$$

As indicated in the figure, root B_* becomes the adjustment level to which biomass trajectory $B(t)$ will trend when F is less than critical quantity $4m/B_\infty$ (and obviously, $B(t)$ trends to B_∞ in Equation (7) when F is zero). The system is governed by the positive branch of Equation (6) when $\dot{Y} < \dot{P}$ (in which case, $\dot{B} > 0$), and by the negative branch of Equation (6) when $\dot{Y} > \dot{P}$ (in which case, $\dot{B} < 0$). But this partitioning of F into subranges for negative or positive $\dot{B}$ is a density-dependent process. Although we must have $F < 4m/B_\infty$ for positive B_*, the values of F on that range that drive the stock either up or down will depend on initial stock size B_0. To insure, for arbitrary B_0, that $\dot{Y} < \dot{P}$ in Equation (6), mortality F must have a value such that

$$0 < F < \frac{4m}{B_\infty}\left[1 - \frac{B_0}{B_\infty}\right],$$

in which case $B(t)$ increases from initial value B_0 towards a higher adjustment level B_*. But for any value of F on the interval

$$\frac{4m}{B_\infty}\left[1 - \frac{B_0}{B_\infty}\right] < F < \frac{4m}{B_\infty},$$

then $\dot{Y} > \dot{P}$ and $B(t)$ decreases from B_0 towards a lower adjustment level B_*.

Figure 3 illustrates the relationship between net productivity (Equation (6)) and the biomass solution (Equation (7)) when

$$F \geq \frac{4m}{B_\infty},$$

in which case the adjustment level of biomass corresponds to the zero root of Equation (6). As indicated by the figure, any mortality F so great as to equal or exceed the quantity $4m/B_\infty$, if maintained, will fish a Graham stock to extinction.

Since Equation (6) governs the relationship between transient biomass and nonequilibrium removal, we look to its solution (Equation (7)) for time delays between equilibria. But the asymptotic behavior of Equation (7) is a minor analytical annoyance to be circumvented here. Let us

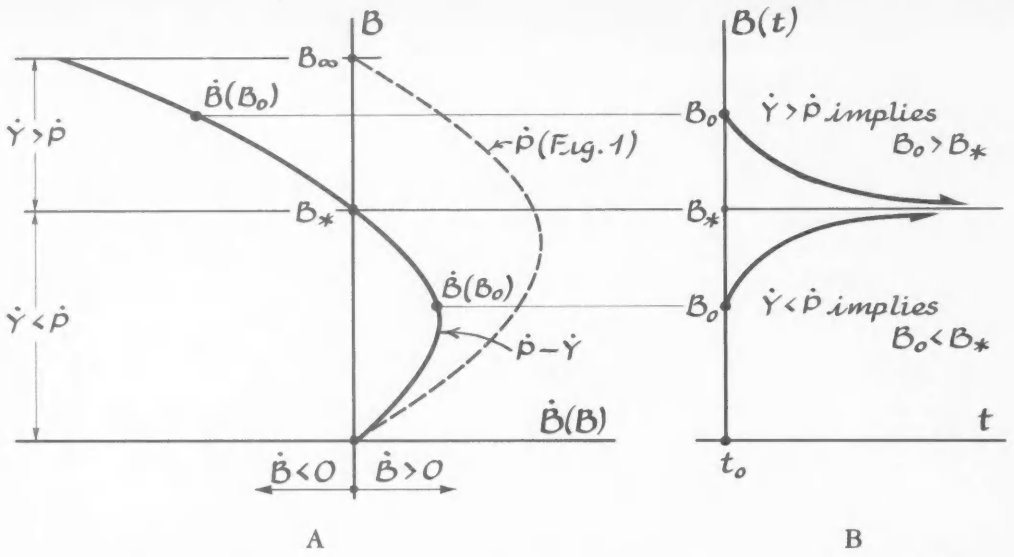


FIGURE 2.—A. Typical phase-plane graph of net productivity $\dot{B} = \dot{P} - \dot{Y}$, Equation (6), the Graham system, with mortality F constrained to the interval $0 < F < 4m/B_\infty$. When removal rate $\dot{Y}$ exceeds latent productivity $\dot{P}$ then $\dot{B} < 0$ and the negative branch of Equation (6) applies. When productivity $\dot{P}$ exceeds removal rate $\dot{Y}$ then $\dot{B} > 0$ and the positive branch applies. B. Typical solution graphs of stock biomass $B(t)$, Equation (7). When $\dot{Y} > \dot{P}$, biomass declines from initial value B_0 towards adjustment level B_*. When $\dot{Y} < \dot{P}$, biomass increases from initial value B_0 towards adjustment level B_*.

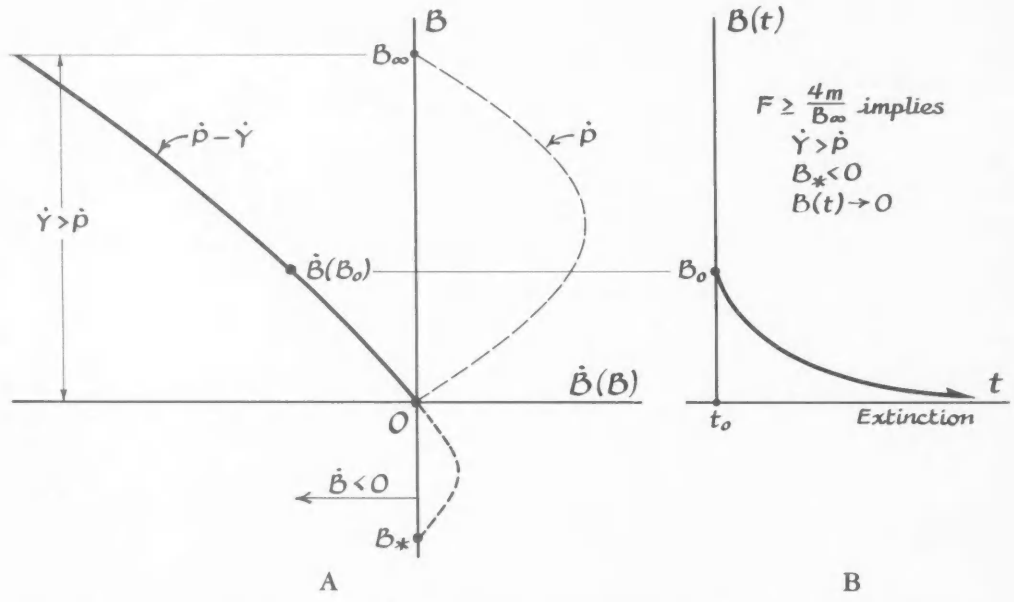


FIGURE 3.—A. Typical graph of net productivity $\dot{B} = \dot{P} - \dot{Y}$, Equation (6), the Graham system, with mortality $F \geq 4m/B_\infty$. For any such value of F, the zero root of Equation (6) applies, removal rate $\dot{Y}$ exceeds latent productivity $\dot{P}$, and $\dot{B} < 0$. B. Typical solution trajectory $B(t)$ of Equation (7) when $F \geq 4m/B_\infty$. Biomass declines from initial value B_0 towards extinction level $B = 0$.

presume that no practical technique of estimation will have a precision of resolution better than some assignable percentage of true stock size, and let us reflect that practical uncertainty in our analysis by expanding the asymptotic bound of Equation (7) to a region of radius $\epsilon \cdot B_*$ around the analytical value of the bound (ϵ being the measure of the uncertainty). Whence, with B_0 and B_1 now signifying initial and adjustment levels, and by supposing that F changes abruptly at time t_0 from value F_0 to some new value F_1, Equation (7) becomes

$$(1 \pm \epsilon) = \frac{1}{1 + C_0 e^{-(4m/B_\infty - F_1)t}},$$

the plus sign applying when $F_1 > F_0$ and the minus sign when $F_1 < F_0$. By setting initial time t_0 arbitrarily at zero,

$$C_0 = \frac{B_1 - B_0}{B_0},$$

and the transition time between initial level B_0 and the ϵ-region at adjustment level B_1 becomes

$$t_{\text{lag}} = \frac{1}{4m/B_\infty - F_1} \ln \left[\frac{(1 \pm \epsilon)(B_1 - B_0)}{-(\pm \epsilon B_0)} \right]. \quad (8)$$

In few commercial fisheries do we expect to see exploitation rates constant over intervals equal to transition times t_{lag}, and in any case we anticipate considerable variation in stock size along the way, owing to chance events. Nevertheless, Equation (8) serves a purpose; it will give us some idea, in a management strategy, of the time delays to be expected in bringing a stock from one general state of exploitation to another through the regulation of mortality F.

To illustrate the particularization of Equation (8), we follow an adaptation by Ricker (1975: 312-315) of Graham's work on demersal stocks of the North Sea. To accommodate our formulation here, parameters for Ricker's adaptation would be

B_∞ = 220,000 tons,
m = 40,300 tons yr^{-1} (the MSY of the model).

With reference to Ricker's illustrations (1975: 312-315), we first calculate the time delay that accompanies a reduction in mortality from F_0 = 0.40 yr^{-1}, corresponding to a stock level of B_0 = 100,000 tons, to a new mortality commencing at reference time zero, of F_1 = 0.20 yr^{-1}. The adjustment level to which $B(t)$ will trend in the transition period is B_1 = 160,000 tons (by setting, in Equation (6), $B = 0$, $F = F_1$ and $B = B_1$. If we now specify the uncertainty in estimation precision as being, say, 5% of true stock size, then Equation (8), with $F_1 < F_0$ and $\epsilon = 0.05$, gives the estimated delay in adjustment as

$$t_{\text{lag}} = \frac{1}{0.533} \ln \left[\frac{(1 - 0.05)(160{,}000 - 100{,}000)}{0.05(100{,}000)} \right]$$
$$= 4.6 \text{ yr.}$$

When the model stock declines between similar levels, the time delay is longer. That is, stock at level B_0 = 160,000 tons, corresponding to the fishing mortality F_0 = 0.20 yr^{-1}, declines to the adjustment level B_1 = 100,000 tons following an increase at $t_0 = 0$ to the new mortality F_1 = 0.40 yr^{-1}. Transition time t_{lag} now becomes

$$t_{\text{lag}} = \frac{1}{0.333} \ln \left[\frac{(1 + 0.05)(100{,}000 - 160{,}000)}{-0.05(160{,}000)} \right]$$
$$= 6.2 \text{ yr.}$$

Yields from transient periods differ considerably from the removals associated with equilibrium states. Obviously, an increase in fishing mortality increases the yield temporarily, and a decrease in fishing mortality decreases the yield temporarily, but the ensuing trends of adjustment will depend, in the context of the Graham system, on the following relationships:

$F < 4m/B_\infty$; stock size $B(t) \to B_*$ (Figure 2), which implies that $\dot{Y} \to FB_*$.
$F \geq 4m/B_\infty$; root $B_* < 0$ and $B(t) \to 0$ (Figure 3) which implies that $\dot{Y} \to 0$.
$F = 2m/B_\infty$; stock size $B(t)$ implies p (p being the biomass level $B_\infty/2$ where maximum latent productivity occurs; Figure 1), which implies that $\dot{Y} \to m$. Accordingly, we may identify parameter m, in any of the rate equations here, with MSY (which, we should remember, is itself a yield rate).

Since, by Equation (4), instantaneous removal varies in time as $\dot{Y}(t) = F(t)B(t)$, then over the course of the adjustment interval that follows an abrupt change in F, yield from a Graham stock will accumulate as

$$Y(t) = (B_\infty - B_*) \ln \left[1 + \frac{B_0}{B_*}\left(e^{(4m/B_\infty - F)t} - 1\right)\right] \tag{9}$$

$$B_* = \left[B_\infty - \frac{F B_\infty{}^2}{4m}\right].$$

ANALYSIS OF THE PELLA-TOMLINSON SYSTEM

As noted in the foregoing section, the maximum latent productivity m of a Graham stock always occurs at a biomass value exactly one-half the unexploited maximum B_∞. In turn, MSY of the equilibrium model must also occur at the stock level $B_\infty/2$. So as to gain control over the locations of those extrema, Pella and Tomlinson (1969) modify the Graham system by writing the differential equation for latent productivity $\dot{P}$ essentially in the form of Equation (2), which, by the customary treatment, has a troublesome, dual formulation owing to the sign changes at $n = 1$ of coefficients c_1, c_2. On the interval $0 < n < 1$ latent productivity in the Pella-Tomlinson system takes the basic form

$$\dot{P} = aB^n - bB \tag{10}$$

(where, for the sake of emphasis, $c_1 = -b$, $c_2 = a$, with a and b positive), but on the interval $n > 1$ latent productivity takes on the basic form

$$\dot{P} = bB - aB^n \tag{11}$$

(where $c_1 = b$, $c_2 = -a$, with a and b positive). In either case, the bound B_∞, the maximum productivity m, and the ordinate p (which governs the biomass level where m occurs), all depend on the numerical value assigned to exponent n. That is, root B_∞ is given by

$$B_\infty = \left[\frac{a}{b}\right]^{1/(1-n)},$$

the ordinate p is determined by

$$p = \left[\frac{an}{b}\right]^{1/(1-n)},$$

while maximum productivity m, by the conventional casting of the model, must be determined from the formula

$$m = \pm \frac{b(1-n)}{n}\left[\frac{an}{b}\right]^{1/(1-n)},$$

the plus sign applying to Equation (10) and the minus sign to Equation (11).

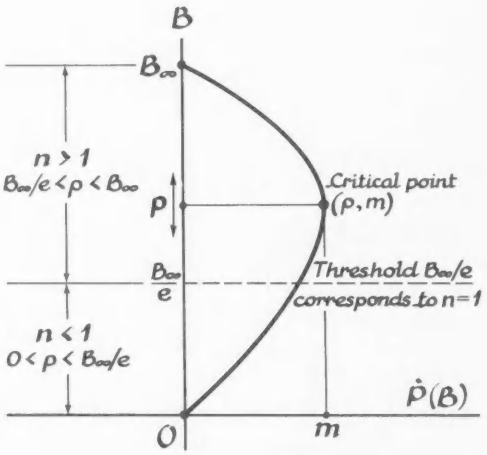


FIGURE 4.—Typical graph of Equation (12), latent productivity $\dot{P}$ as a function of stock size B, the Pella-Tomlinson system.

Coordinate p, in its location with respect to root B_∞, directly reflects the value assigned to exponent n, as indicated by Figure 4. When n takes any value between zero and unity, coordinate p falls on the range between zero and B_∞/e ($\approx 0.3679\, B_\infty$), in which case Equation (10) applies. When n takes any value greater than unity, coordinate p falls on the range between B_∞/e and B_∞, in which case Equation (11) applies. But the coordinate m has no essential dependence on exponent n, and its apparent coupling with n (as indicated by the formulation above) is merely an inconvenient artifact of the conventional analysis. With parameters m and n uncoupled (see Fletcher 1975), the Equations (10) and (11) that govern latent productivity in the Pella-Tomlinson system can be consolidated into the single governing equation

$$\dot{P} = \gamma m \left[\frac{B}{B_\infty}\right] - \gamma m \left[\frac{B}{B_\infty}\right]^n, \tag{12}$$

with γ a purely numerical factor wholly prescribed by n as

$$\gamma = \frac{n^{n/(n-1)}}{n-1}. \qquad (13)$$

With the coefficients so cast, the sign reversals at turning point $n = 1$ become automatic. In consequence, the consolidated interval of definition for n becomes $0 < n < \infty$ (the point $n = 1$ being a removable singularity). With parameter m thus separated from n in Equation (12), the undetermined exponent n can be defined solely by the fraction p/B_∞ in the relationship

$$\frac{p}{B_\infty} = n^{1/(1-n)}. \qquad (14)$$

Consolidated Equation (12) now takes on the role in the Pella-Tomlinson system that Equation (1a) takes on in the Graham system. In fact, when $n = 2$, Equation (12) reduces to Equation (1a), in which case $\gamma = 4$ and $p/B_\infty = \frac{1}{2}$. As an interesting aside here, we note that Equation (12), at the turning point $n = 1$, takes on the form

$$\dot{P} = -e\,m \left[\frac{B}{B_\infty}\right] \ln \left[\frac{B}{B_\infty}\right]$$

(e being Napier's constant), while ratio (14), in the limit as $n \to 1$, has the value

$$\frac{p}{B_\infty} = \frac{1}{e}.$$

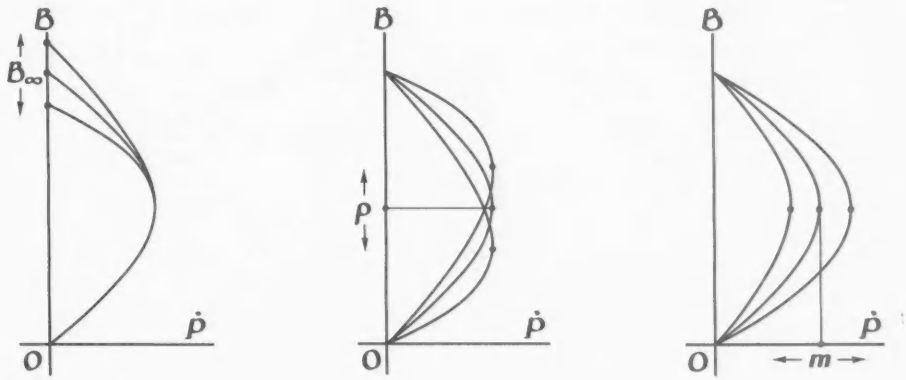
In fact, Fox (1970) constructed a stock-production model around this special case, but since the ratio p/B_∞ has the fixed value $1/e$, Fox's model "has as rigid a form as the Graham model" (Ricker 1975: 331).

Quantities m, p, and B_∞ constitute a complete, minimum set of independent parameters for latent productivity in the Pella-Tomlinson system. Collectively they control the behavior of governing Equation (12), but the influence of any one parameter remains independent of the remaining two. Figure 5 illustrates their separate effects on the graph of Equation (12).

By appealing to the same piecewise constraints that enter the Graham productivity equations, we substitute Equation (12) into the general productivity formula (Equation (5)) and net productivity in the Pella-Tomlinson system becomes

$$\dot{B} = \gamma m \left[\frac{B}{B_\infty}\right] - \gamma m \left[\frac{B}{B_\infty}\right] - FB. \qquad (15)$$

And over any time interval, however brief, that mortality F might be presumed to have a fixed value, biomass variable B in Equation (15) has the general time-dependent solution



B_∞: unexploited stock level [the nonzero root of Equation (12)].

p: biomass level for maximum productivity [the coordinate of B in Equation (12) where m occurs].

m: maximum productivity [the extremum coordinate P_{max} in Equation (12)].

FIGURE 5.—The graph of Equation (12), latent productivity in the Pella-Tomlinson system, as controlled by independent parameters m, p, and B_∞.

$$B(t) = \left[B_*^{1-n} + C \exp\left((\gamma m/B_\infty - F)(1-n)\, t\right)\right]^{1/(1-n)}, \tag{16}$$

$$B_* = \left[\frac{\gamma m}{\gamma m - F B_\infty}\right]^{1/(1-n)} B_\infty.$$

By setting initial time t_0 arbitrarily at zero, the integration constant C in Equation (16) becomes

$$C = B_0^{1-n} - B_*^{1-n}.$$

Biomass Equation (16) will apply immediately upon a change in F and remain valid thereafter for the time that F remains constant. Over such time, population biomass will trend up or down in accord with Equation (16) from initial size B_0 towards adjustment level B_*. Should nonzero root B_* be negative (which is possible only when $n > 1$), then the adjustment level corresponds to the zero root of Equation (15) and the population tends to extinction by Equation (16).

The critical relationships between fishing mortality, productivity, and time-dependent yield rate in the Pella-Tomlinson system are considerably more complex than the relationships between F, $\dot{P}$, and $\dot{Y}$ in the Graham system. Figure 6 illustrates the behavior of $\dot{P} - \dot{Y}$ when $n < 1$, and Figures 7 and 8 illustrate $\dot{P} - \dot{Y}$ when $n > 1$. The ratio $\gamma m/B_\infty$ becomes the critical quantity in the Pella-Tomlinson system ($4m/B_\infty$ being its counterpart in the Graham system).

As indicated by Figure 6, the biomass level p where maximum productivity occurs must lie on the range $0 < p < B_\infty/e$ when $0 < n < 1$. And when n takes any such value, the corresponding Pella-Tomlinson stock will exhibit nonzero adjustment levels of biomass for all values of fishing mortality however large; such a stock cannot be fished to extinction. That is, nonzero root B_* of Equation (15) will always have a positive value when $0 < n < 1$, its range of variation being $0 < B_* \leq B_\infty$ for F unrestricted on $0 \leq F < \infty$. But F is partitioned into subranges accordingly as $\dot{Y} < \dot{P}$ or $\dot{Y} > \dot{P}$. And those values of F, for which $B(t)$ either increases or decreases to B_*, depend on the critical ratio $\gamma m/B_\infty$ and initial biomass value B_0. To insure, for arbi-

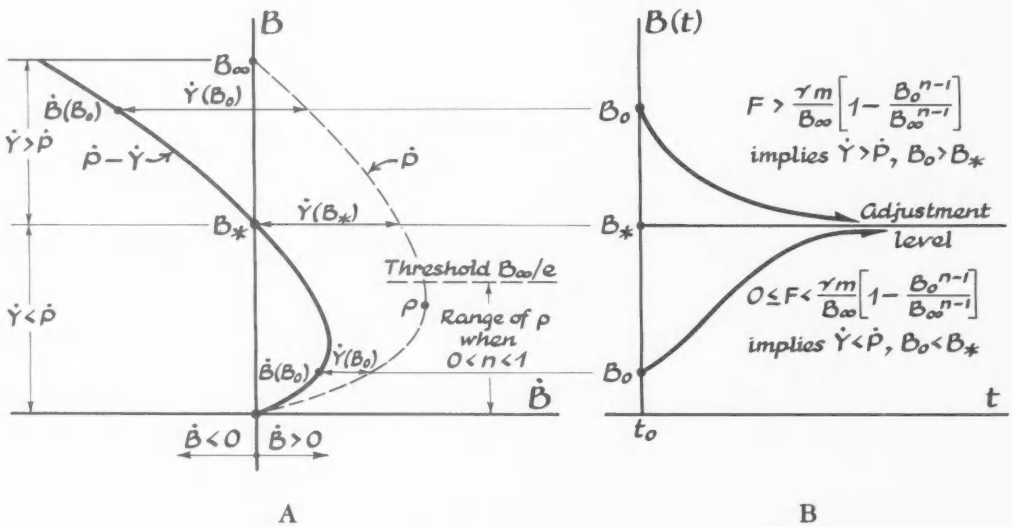


FIGURE 6.—A. Typical phase-plane graph of net productivity Equation (15), the Pella-Tomlinson system, for values of n where $0 < n < 1$. For any such value of n, root B_* of Equation (15) is always positive irrespective of the magnitude of F. Should removal rate $\dot{Y}$ exceed latent productivity $\dot{P}$, then $\dot{B} < 0$ and the negative branch of Equation (15) applies. Should $\dot{P}$ exceed removal rate $\dot{Y}$, then $\dot{B} > 0$ and the positive branch applies. B. Typical solution graphs of stock biomass $B(t)$, Equation (16), when $0 < n < 1$. Should $\dot{Y} > \dot{P}$, biomass declines from initial value B_0 towards adjustment level B_*. But when $\dot{Y} < \dot{P}$, biomass increases from B_0 towards B_*.

trary B_0, that $\dot{Y} < \dot{P}$ in Equation (15), mortality F must have a value such that

$$0 \leq F < \frac{\gamma m}{B_\infty}\left[1 - \frac{{B_0}^{n-1}}{{B_\infty}^{n-1}}\right],$$

in which case $\dot{B} > 0$ and the positive branch of Equation (15) applies. Trajectory $B(t)$ then increases, in accord with Equation (16), from initial value B_0 towards a higher adjustment level B_*. But for any value of F such that

$$F > \frac{\gamma m}{B_\infty}\left[1 - \frac{{B_0}^{n-1}}{{B_\infty}^{n-1}}\right],$$

then $\dot{Y} > \dot{P}$ and the negative branch of Equation (15) applies; trajectory $B(t)$ decreases from B_0 towards a lower adjustment level B_*.

Although the sign of $\dot{B}$ and the consequential course of $B(t)$ is a density-dependent process for given F, we should note here that when

$$F = \left[\frac{n-1}{n}\right]\frac{\gamma m}{B_\infty}, \qquad (17)$$

then $B(t) \rightarrow \dot{Y}$ and $\rightarrow m$, irrespective of initial conditions. Accordingly, we may identify parameter m with MSY in any of the (reformulated) rate equations of the system.

As indicated by Figures 7 and 8, the biomass level p where m occurs must lie on the range $B_\infty/e < p < B_\infty$ when $n > 1$. And with n so prescribed, root B_* of Equation (15) may have positive or negative values accordingly as F has a value less or greater than the critical ratio $\gamma m/B_\infty$. Figure 7 illustrates the behavior of Equations (15) and (16) for the constraints

$$n > 1$$
$$0 \leq F < \frac{\gamma m}{B_\infty}$$
$$0 < B_* \leq B_\infty,$$

in which case, root B_* of Equation (15) becomes the adjustment level such that $B(t) \rightarrow B_*$ by Equation (16). But whether $B(t)$ trends up or down to B_* depends on the further partitioning of F with respect to initial biomass value B_0. To insure, for arbitrary B_0, that $\dot{Y} < \dot{P}$ in Equation (15), mortality F must be further constrained to the interval

$$0 \leq F < \frac{\gamma m}{B_\infty}\left[1 - \frac{{B_0}^{n-1}}{{B_\infty}^{n-1}}\right];$$

thus $\dot{B} > 0$ and the positive branch of Equation (15) applies as indicated by Figure 7a. Trajectory $B(t)$ then increases, in accord with Equation (16), from initial value B_0 towards a higher adjustment level B_*, as indicated by the lower curve of Figure 7b. But for any value of F on the interval

$$\frac{\gamma m}{B_\infty}\left[1 - \frac{{B_0}^{n-1}}{{B_\infty}^{n-1}}\right] < F < \frac{\gamma m}{B_\infty},$$

then $\dot{Y} > \dot{P}$, $\dot{B} < 0$, and the negative branch of Equation (15) applies; trajectory $B(t)$ decreases from B_0 towards a lower adjustment level B_* as indicated by the upper curve of Figure 7b.

Should mortality F equal or exceed the critical ratio $\gamma m/B_\infty$ in a Pella-Tomlinson system where n exceeds unity, the corresponding stock, over sufficient time, will trend to extinction. Figure 8 illustrates the behavior of Equations (15) and (16) for the constraints

$$n > 1$$
$$F \geq \frac{\gamma m}{B_\infty}$$
$$B_* \leq 0,$$

in which case the zero root of Equation (15) applies, and we have $\dot{B} < 0$ and $B(t) \rightarrow 0$, irrespective of initial conditions.

By expanding the asymptotic bound of Equation (16) to a region of radius $\epsilon \cdot B_*$, and by appealing to arguments similar to those that led to the delay estimate (Equation (8)) of the Graham system, we calculate from Equation (16) the transition times for a Pella-Tomlinson stock as being

$$t_{\text{lag}} = \frac{B_\infty}{(1-n)(\gamma m - F_1 B_\infty)} \ln\left[\frac{1 - (1 \pm \epsilon)^{1-n}}{1 - (B_0/B_1)^{1-n}}\right] \qquad (18)$$

where ϵ represents the imprecision of stock-abundance estimates, and where B_0 and B_1 signify initial and adjustment levels as they correspond to mortality values F_0 and F_1. Again we suppose that F changes abruptly at zero reference time from value F_0 to the new value F_1, the plus sign of Equation (18) applying when $F_1 > F_0$ and the minus sign when $F_1 < F_0$.

By Equation (4) and the assumption that F varies in time by taking on fixed values of finite duration, we can write the transient yield rate for the Pella-Tomlinson system in the consolidated form

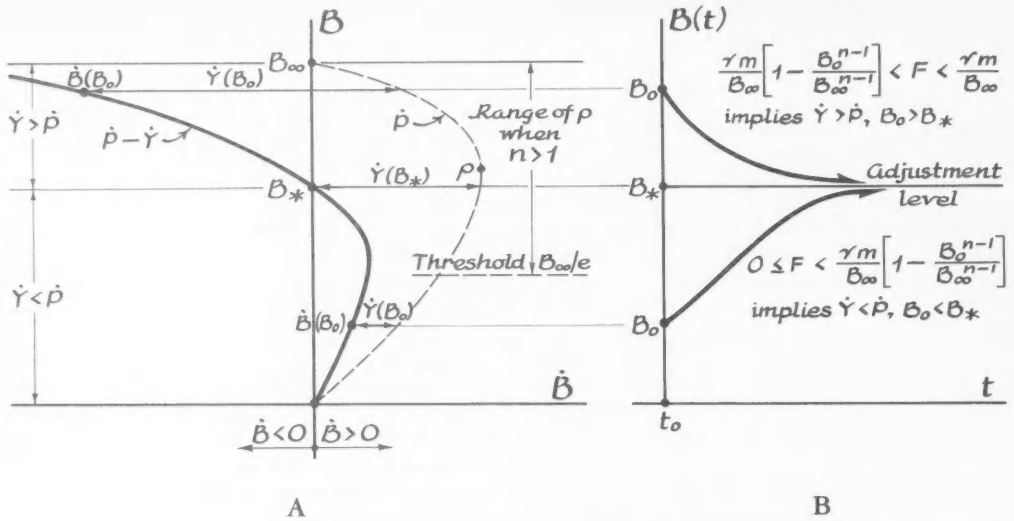


FIGURE 7.—A. Typical phase-plane graph of Equation (15) when $n>1$ and $F<\gamma m/B_\infty$, in which case root $B_*>0$. Should $\dot{Y}>\dot{P}$, the negative branch of Equation (15) applies; should $\dot{Y}<\dot{P}$, the positive branch applies. B. Typical solution trajectories, Equation (16), when $n>1$ and $F<\gamma m/B_\infty$. Should $\dot{Y}>\dot{P}$, biomass trajectory $B(t)$ declines from initial value B_0 toward adjustment level B_*. Should $\dot{Y}<\dot{P}$, $B(t)$ increases from B_0 toward B_*.

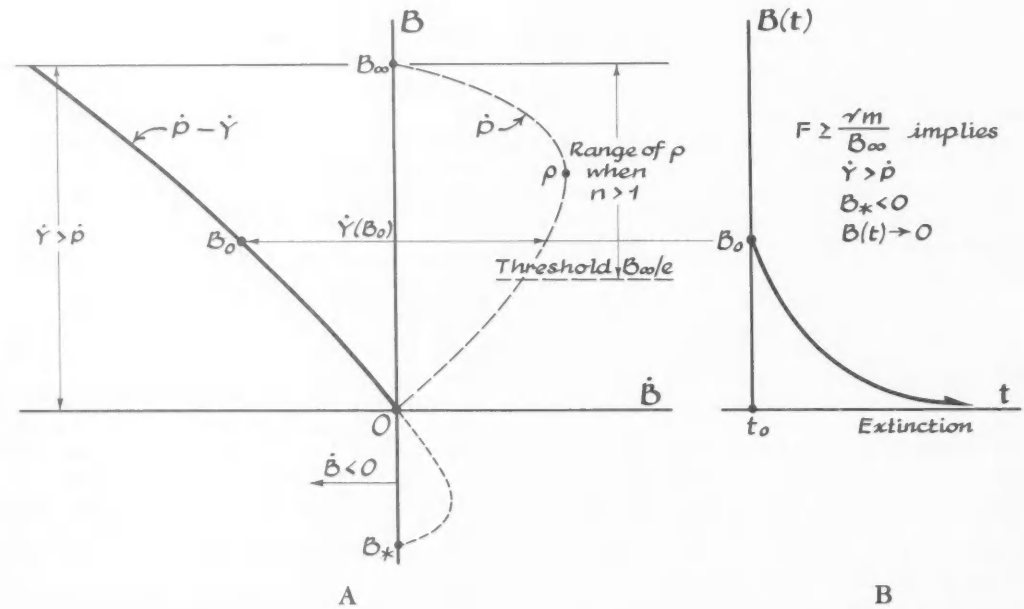


FIGURE 8.—A. Phase-plane graph of net productivity Equation (15) when $n>1$ and $F \ge \gamma m/B_\infty$. For any such combination of n and F, $B_*<0$ and the zero root of Equation (15) applies. B. Typical solution trajectory, Equation (16), when $n>1$ and $F \ge \gamma m/B_\infty$, in which case the stock declines from initial value B_0 towards extinction.

$$\dot{Y}(t) = FB_* \left[1 - \left(1 - (B_0/B_*)^{1-n}\right) \exp\left((\gamma m/B_\infty - F)(1-n)\, t\right)\right]^{1/(1-n)} \quad (19)$$

which is valid for all values of n save $n = 1$. Owing to the range of definition on exponent $1/1-n$, I have not found a closed form for the general time integral of Equation (19) (although existence is fairly easy to show for n positive and either less or greater than unity). But the usefulness of the analysis does not suffer too greatly for that omission, since one may accommodate Equation (19) to a numerical equation solver for finite measures of yield δY on associated intervals δt.

When F changes abruptly (as we have assumed throughout), yield rate $\dot{Y}$ changes abruptly, but the ensuing trends of adjustment are governed, in the Pella-Tomlinson system, by the following relationships:

$0 < n < 1$:
$0 < F < \infty$; stock size $B(t) \rightarrow B_*$ (Figure 6), which implies that $\dot{Y} \rightarrow FB_*$.
$n > 1$:
$F < \gamma m/B_\infty$; stock size $B(t) \rightarrow B_*$ (Figure 7), which implies that $\dot{Y} \rightarrow FB_*$.
$F \geq \gamma m/B_\infty$; stock size $B(t) \rightarrow 0$ (Figure 8), which implies that $\dot{Y} \rightarrow 0$.
$n > 0$ (both ranges):
$F = (1-1/n)\gamma m/B_\infty$; stock size $B(t) \rightarrow p$, which implies that $\dot{Y} \rightarrow m$ (and we may identify maximum latent productivity m with maximum yield rate in any of the time-dependent formulations of the analysis).

The quantity $\gamma m/B_\infty$, which plays such a prominent role in the analysis, can be identified as the "intrinsic growth rate" of the stock whenever exponent $n > 1$, in direct analogy to quantity k of the Graham system (and, in fact, with $n = 2$, then $\gamma = 4$ and $4m/B_\infty \equiv k$). But as a consequence of the indeterminate power form of the Pella-Tomlinson system and the switching of coefficient signs in the governing equations, the intrinsic growth rate turns out to be density-dependent when n takes on values between zero and unity. That is, by Equation (12), the intrinsic rate (if we may call it so) has the form

$$-\frac{\gamma m}{B_\infty} B^{n-1}$$

when n falls on the interval $0 < n < 1$ (in which case, $\gamma < 0$).

DISCUSSION

Any nonlinear stock-production system may be restructured along the lines of the critical-point analysis described in the foregoing sections; such a treatment will generate parametric variables most likely to be those essential to management analysis. A synopsis of the parameters that appear in the restructured Graham and Pella-Tomlinson systems is given by Table 1.

TABLE 1.—Parameters of the restructured Graham and Pella-Tomlinson systems as they apply to management components.

Management components	Control parameters: Graham system	Control parameters: Pella-Tomlinson system
Maximum stock size	B_∞	B_∞
Maximum productivity (corresponds to MSY)	m	m
Stock size for maximum productivity (the "optimum" stock size)	$B_\infty/2$ (fixed)	p
Ratio p/B_∞	½(fixed)	$n^{1/(1-n)}$
Fishing mortality	F	F
General adjustment level (consult text for mortality conditions)	B_* or 0	B_* or 0
Fishing mortality for adjustment level p (the "optimum" F)	$2m/B_\infty$	$(1 - 1/n)\ \gamma m/B_\infty$
Graph curvature	fixed	n

For optimization procedures on the Graham system, the essential parameters are $\{F, m, B_\infty\}$ augmented by the auxiliary parameters B_0 and B_*. For the Pella-Tomlinson system we may choose the combination $\{F, m, p, B_\infty\}$ or the combination $\{F, m, n, B_\infty\}$, either of which constitutes an essential set of mutually independent parameters. In the first set, p and B_∞ determine n; in the second, n and B_∞ determine p. The relationships in either case are governed by Equation (14).

Although the parametric influence of n is wholly prescribed by the ratio p/B_∞, exponent n also determines the curvature of all graphs of the Pella-Tomlinson system. Therefore, when the particularization of the system depends primarily on general curve fitting, the likelihood always exists that ill-determination of parameters will follow,

owing to stochastic displacement of datum points at biomass levels remote from locations p and B_∞. As revealed by Equation (14), exponent n is quite unstable to small perturbations in the ratio p/B_∞. The variational response in n exceeds the perturbation in p/B_∞ by an order of magnitude near $n = 1$, and the instability increases as $p/B_\infty \rightarrow 1$. But the location of p with respect to B_∞ is far more critical to management analysis than graph curvature and its associated "good fit," since, to the left of p, the stock produces biomass at a positively accelerated rate, while to the right of p productivity decelerates.

The trait of degeneracy in the system has been noted by Pella and Tomlinson (1969) and by Fox (1971, 1975), but the exact relationships between exponent n and the quantities m, p, and B_∞ have been obscured heretofore by the conventional castings of the system. With the restructured governing equations and the explicit formulations of critical parameters, much of the statistical degeneracy associated with previous routines can be constrained. And since the management parameters appear directly in the equations of the system, their variances can be calculated directly in the estimation procedure and appeals to indirect methods are avoided.

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TROPHIC RELATIONSHIPS IN JUVENILES OF THREE SPECIES OF SPARID FISHES IN THE SOUTH AFRICAN MARINE LITTORAL

M. S. CHRISTENSEN[1]

ABSTRACT

The feeding habits of three sparids, *Diplodus sargus*, *D. cervinus*, and *Sarpa salpa*, were studied. Juveniles of these fishes occur commonly in the intertidal and immediately subtidal regions of southeast Africa, while adults were only observed in these zones at high tide. Small juvenile *D. sargus* feed largely on harpacticoid copepods, amphipods, and, in spring and early summer, cirripede nauplii, chironomid larvae, and an unidentified trochophore larva. Larger individuals mainly take amphipods and green algae. Successive size classes of *D. cervinus* feed mainly on harpacticoid copepods and chironomid larvae, the shrimp *Palaemon pacificus*, amphipods, and then polychaetes. *Sarpa salpa* ingest harpacticoids when small, diatoms and red algae as a large juvenile, and red and green algae as an adult. Corresponding changes in gut length and dentition are reported for *S. salpa*.

Marked ecological separation of the three species was observed. Small juveniles appear at different times of the year and feed on different foods (dietary and temporal separation). Larger juveniles and subadults have different diets or feed in separate parts of the littoral zone (behavioral, dietary, and spatial separation).

A brief review of methods of analyzing stomach contents is included and it is suggested that a combination of points and ranking indices would be the most valuable. The method, here termed the comparative feeding index, is described.

The food and feeding relationships of fishes in the intertidal zone of South Africa are poorly documented and the results are largely qualitative. The most important of these studies deal with one or two species of the families Gobiidae (Pitt-Kennedy[2]), Sparidae (Hutchings[3]), Cheilodactylidae (Butler[4]), and Gobiesocidae (Stobbs[5]).

Three species of sparids were investigated in the present survey, *Sarpa salpa* (Linnaeus 1758), *Diplodus sargus* (Linnaeus 1758), and *D. cervinus* (Lowe 1838). Barnard (1927), Smith (1965), and Hutchings (see footnote 3) described *S. salpa* (strepie) as being primarily a herbivore, whereas Talbot (1954) found the fish to be omnivorous. The latter study was made in an estuary, however, where algae are generally less abundant than in the intertidal region. *Diplodus sargus* (blacktail) is described as being an omnivore (Biden 1954; Talbot 1954; Smith 1965), as is *D. cervinus* (zebra). Little, however, has been published on the food and feeding habits of the juveniles of these three species, although they are abundant in the intertidal and immediately subtidal regions of this coast.

The objectives of this study have, therefore, been to determine: 1) the diet of juveniles of these three species; 2) how feeding changes with age and season; 3) the degree of overlap between species, possibly resulting in competition; 4) recruitment times and approximate growth rates of the fish; and 5) the relationship between dentition, gross gut morphology, and diet.

During the course of this study, existing methods of fish feeding analysis were found to be inadequate and a new technique is described which overcomes some of the problems.

MATERIALS AND METHODS

Fish were collected from February to December 1975 at 2-wk intervals during spring tide, in spite of the possibility of introducing biases, as diving

[1]J. L. B. Smith Institute of Ichthyology, Rhodes University, P.O. Box 94, Grahamstown, 6140, South Africa.

[2]Pitt-Kennedy, S. 1968. A preliminary investigation of feeding in two gobies *Coryphopterous caffer* (Günther) and *C. nudiceps* (C. and V.) with notes on their sexual maturity. Unpubl. honors proj., 39 p. Zool. Dep., Univ. Cape Town, S. Afr.

[3]Hutchings, L. 1968. A preliminary investigation into the diets of two littoral teleosts, *Sarpa salpa* (Linnaeus) and *Puchymetopon blochii* (Valenciennes), with notes on their biology. Unpubl. honors proj., 25 p. Zool. Dep., Univ. Cape Town, S. Afr.

[4]Butler, G. S. 1975. An investigation into the biology of two inter and infratidal species of Cheilodactylidae (Pisces: Teleostei). Unpubl. honors proj., 29 p. Zool. Dep., Rhodes Univ., Grahamstown, S. Afr.

[5]Stobbs, R. E. In preparation. Preliminary investigations into the feeding behaviour and food preferences of *Chorisochismus dentex* (Pisces: Gobiesocidae).

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conditions were most suitable at this time. Hand nets were used in the intertidal pools and multiprong spear guns in the subtidal area. Hook and line, poison, traps, and gill nets were not used as further biases may be induced to the feeding data (Randall 1967). Fish collected with hand nets were immediately placed in a 10% Formalin[6] solution, whereas this procedure was delayed for up to 1½ h in the case of those taken by spear. It was concluded that death stops or greatly slows digestion, as the stomach contents were found to be in an equally digested state in both groups on later analysis. This has also been observed by Hobson (1974).

The fish were left in Formalin for 10 to 14 days. This time period was maintained throughout to standardize any length and weight changes induced by the fixative (up to 5%, Royce 1972). About 10 scales were removed from under the pectoral fin and cleaned with a camel hair brush after having been soaked overnight in water with a trace of carbolic acid (Pinkas 1966). They were mounted dry and examined over a white background using a low-power binocular microscope. Standard lengths to the nearest millimeter were taken and the stomach removed and placed in 45% n-propyl alcohol.

The stomach is here defined as that part of the gut between the last gill arch and the gut caecae. The intestines were not examined as some food items are more resistant to digestion than others, with resultant biases as one moves along the gut (Randall 1967; Kionka and Windell 1972; Gannon 1976). Food items were identified to species where possible.

Numerous methods have been employed in analyzing the food habits of fishes and volumetric and gravimetric techniques are being more widely used today with the current trend towards greater accuracy (Windell 1971). Both suffer from the same limitation in that digestion of the food both reduces its volume and weight. This has resulted in the use of reconstructed weights and volumes where the live weight and/or volume is back-calculated from a measureable parameter, e.g., carapace length (M. Bruton, pers. commun.). In this particular study some of the fish had fed on diatoms and it is not feasible to determine the volume of such small items (Windell 1971). Similarly, the reconstructed weight could not be determined as a sample of monospecific, uncontaminated diatoms is impracticable to obtain and contains an indeterminate number of dead frustules which varies from sample to sample (Round 1971).

In such cases, the points (Swynnerton and Worthington 1940) and ranking index methods (Hobson and Chess 1973) would appear to be more satisfactory and were initially used in the present study. The points system was modified by Frost (1943) and subsequently by Hynes (1950) to take into account gut fullness, 30 points being allotted when the stomach was distended, 20 when full, 10 when half full, and so on. One, two, four, eight, or sixteen points were assigned to each food item rather than fractions of the total allotted to each stomach in proportion to their volumes. This is an artificial situation and the method was revised as described below.

After removal, the stomach is allotted between 0 and 30 points in proportion to its fullness. This is very subjective but overcome to some extent when large numbers of guts are handled. The contents are then sorted, identified, and the percentage volume estimated for each food item with the aid of Data Sheet No. 6 of Geotimes.[7] All estimations are made with the organisms spread out to an even depth throughout the microscope field or equivalent surface. The total number of points allocated to that stomach is then subdivided amongst the food items in proportion to their percentage volumes. The points gained by each food item are summed for the total sample of fish and the mean calculated. The values are then scaled down to a percentage to give the dietary composition of the fish examined. In the case of the ranking index (RI), the volume is estimated as above and the mean calculated for each food item per fish. The mean volume is then multiplied by the ratio of the number of fish containing that item to the total sampled.

The points method, however, places too much weight on single food items that have been fed on to distension by a few fish, whereas the RI method fails to consider stomach fullness. It is therefore suggested that an alternative, here termed the comparative feeding index (CFI), would be more suitable as it takes into account all three factors, i.e., the volume, fullness, and frequency of occurrence of each food item. The method involves the

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[7]Available from the American Geological Institute, 2101 Constitution Avenue, N.W., Washington, D.C.

allotment of points to each food organism as described above and the mean value per fish is then multiplied by the percentage of the total sample of fish that contain that item. As can be seen, the CFI combines the properties of both points and RI methods and thus reduces to some extent the effect of the problems discussed.

The diet of these fish was also determined by the occurrence method (Hynes 1950) as this indicates the feeding preferences rather than the food's volumetric value. This is determined as the percentage of fish in the sample analysed which contain that particular food item.

The dietary composition of *D. sargus* was analysed for the winter (February-July) and summer (August-December) periods, as it was found to be seasonal. This was not done for the other two species, as feeding seasonality is synonymous in these fish with the change in diet with age, as they exhibit discontinuous recruitment.

All skeletal material was cleared and stained using the trypsin maceration, alizarin stain method of Taylor (1967). The gut was dissected out in the same specimens, drawn and measured, and the gut length to standard length ratio (G/S) was calculated as in Weatherly (1972).

STUDY AREA

The study area is situated about 3.2 km north of Kleinemonde in the eastern Cape and is known locally as Clayton's Rocks (Figure 1). The shoreline consists of a gently shelving, sandy beach with broken rocky areas of varying extent.

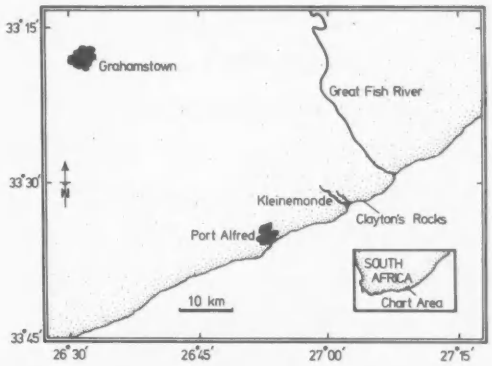

FIGURE 1.—The study area in the Eastern Cape Province, South Africa. Adapted from Topographical Chart 3326, Grahamstown.

The smaller rocky outcrops are continually covered and uncovered by sand, as the beach is unstable and backed by large, shifting sand dunes which move at right angles along the coast. The rocky area under study is made up of sandstone which strikes east-west and dips steeply southwards. This has resulted in the development of gullies and pools partially sheltered from wave action by ridges of resistant rock (Figure 2). The maximum collection depth at the seaward edge of the gullies was 3 m at low tide.

Environmental conditions vary greatly and salinities may fall to 25‰ at low tide, which is caused by freshwater seepage into the pools from springs in the beach. During the day, at low tide, surface water temperatures have been recorded ranging from 26° (summer) to 15°C (winter) in the intertidal and from 22° (summer) to 14°C (winter) in the open sea.

The other major fish species coexisting in the study area are listed below with their general biological characteristics, where known.

ARIIDAE

Tachysurus feliceps: occurs singly, as a juvenile, in crevices.

SPARIDAE

Lithognathus lithognathus: occurs in small groups of juveniles.

Rhabdosargus holubi: juveniles, in small groups.

Sparodon durbanensis: juveniles, observed from October to March, either singly or in small groups.

CHEILODACTYLIDAE

Chirodactylus brachydactylus: as juveniles and subadults, singly, mainly from June to November.

MUGILIDAE

Unidentified species: occur all year round as juveniles.

CLINIDAE

Clinus cottoides: a purely intertidal species, lives in weed, juveniles appeared about June/July.

Clinus superciliosus: lives in weed, juveniles only observed in November/December.

GOBIIDAE

Caffrogobius caffer: intertidal species, juveniles seen from June to November.

TETRAODONTIDAE

Amblyrhyncotes honckenii: singly or in small groups.

FIGURE 2.—The study site at Clayton's Rocks.

RECRUITMENT AND GROWTH

Diplodus sargus

The monthly and total length-frequency distribution is given in Figure 3. The lumped sample shows a mode in the 10- to 20-mm size class, indicating that larger fish tend to emigrate to deeper water. The juveniles appear in the littoral zone when between 9 and 10 mm standard length (SL), and leave when about 90 mm long. It appears that large fish utilize the intertidal area at high tide as two fish of 107 and 108 mm SL were collected in the intertidal area some 2 h after low tide and another 164 mm long was collected 3 h after low tide.

Visibility was <15 cm in the pools of the research area during September, October, and December due to flooding of the Fish River. No dives could be made during this period in the subtidal area with the result that fish >40 mm were not collected.

Recruitment of the juveniles into the littoral appeared to be relatively constant as no monthly peaks of abundance were found during the survey. This tends to confirm Biden's (1954) suggestion that females of this species spawn throughout the year, though mainly in summer.

No monthly modes could be followed over the period of study as it is a continuously recruiting

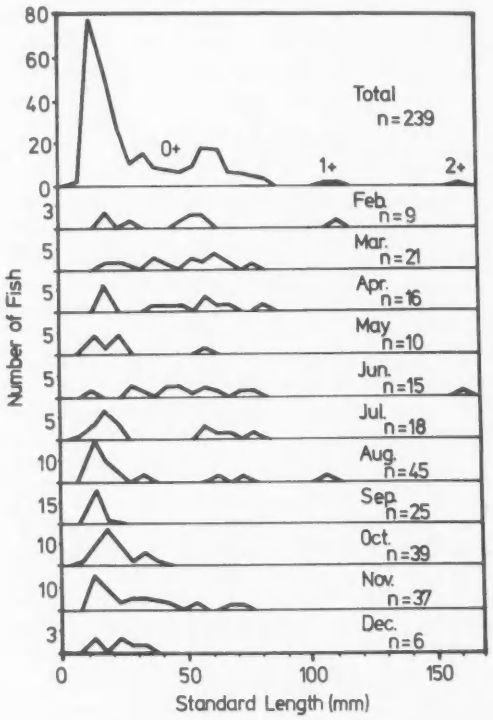

FIGURE 3.—Monthly and total length-frequency distribution of *Diplodus sargus*, showing three age-classes (0+, 1+, and 2+).

population and so growth rates were not estimated. The age of three immature specimens was determined as being 1+ years old (107 and 108 mm SL) and 2+ years old (164 mm SL).

Diplodus cervinus

The length-frequency distribution is given in Figure 4. The total pooled sample shows that this species first appears in the littoral zone when about 8 mm long and leaves again when about 140 mm long. Large fish were observed to move into the intertidal area after low tide, as was the case with *D. Sargus*, but no specimens were obtained.

Monthly modes were observed, which are age-classes 0+, 1+, and 2+ (Figure 4). Recruitment of juveniles into the tide pools is discontinuous, occurring between August and November, with a peak in October. Two fish sampled in August (132 and 129 mm SL) had just formed the second ring, giving the approximate time of scale-ring formation. The estimated average growth rate as determined for mode 1+ is 45 mm from February to December, which is about 54 mm/yr.

Sarpa salpa

The length-frequency distribution shows that the majority of the population is from 9 to 45 mm SL (Figure 5). The juveniles appear in the intertidal when ≥9 mm, and fish >100 mm were never observed in the littoral at low tide; two specimens of age-class 2+ were collected 4 h after low tide.

Three age-classes were observed, labelled as 0+, 1+, and 2+. Recruitment of juveniles into the tide pools is discontinuous, occurring between June and September. Age-classes 1+ and 2+ were approximately ¾ and 1½ yr old, respectively, when sampled. The time of scale-ring formation is then likely to have been about June. The average growth rate is estimated to be 45 mm in 5 mo, or 108 mm/yr for the age-class 0+. Two fish were obtained in April 1976 with lengths of 68 and 76 mm, which indicates that the estimate may be slightly high, the predicted length being 81 mm.

DIETARY COMPOSITION

The composition of the diet is illustrated by occurrence and CFI values scaled down to percentages.

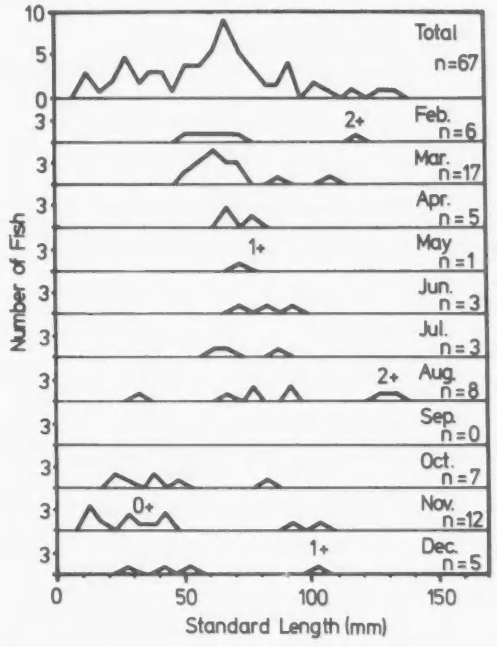

FIGURE 4.—Monthly and total length-frequency distribution of *Diplodus cervinus*, showing three age-classes (0+, 1+, and 2+).

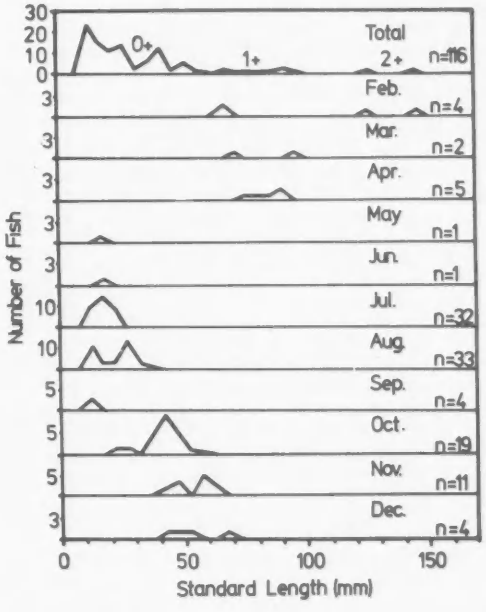

FIGURE 5.—Monthly and total length-frequency distribution of *Sarpa salpa*, showing three age-classes (0+, 1+, and 2+).

Diplodus sargus

Winter Feeding

The diet is composed mainly of harpacticoid copepods, amphipods, algae, isopods, polychaetes, and ostracods (Figure 6; Table 1, n = 88).

The diet of the smallest size class (5-15 mm) is composed almost equally of harpacticoid copepods and amphipods, but the percentage consumed of the former increases in the next size class whereas that of the latter decreases. The diet remained similar in the following two size classes. In the 35- to 50-mm size class, the fish fed little on harpacticoid copepods, the diet being largely composed of amphipods. The situation was similar in the largest size class, although algae and polychaetes were increasingly taken.

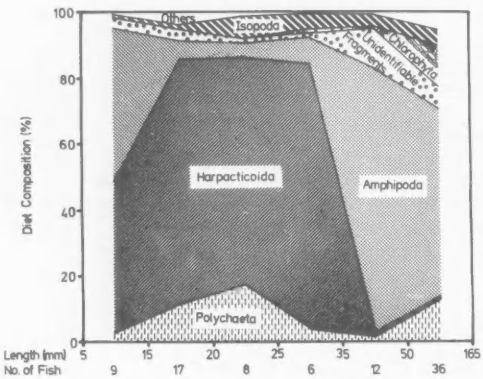

FIGURE 6.—Changes in diet with length of *Diplodus sargus*, collected between February and July 1975, as shown by the comparative feeding index. Food items included in Others are: brachyurans, crab zoaea, diatoms, echinoderms, hydrozoans, leptostracans, molluscs, mysidaceans, *Palaemon pacificus*, rhydophytan algae, sand, and unidentifiable animal fragments.

Summer Feeding

Although similar to the winter diet, chironomid larvae, diatoms, crab zoaea, and leptostracans are more significant. Cirripede nauplii and an unidentified trochophore larva were also commonly taken, and these were not found in winter specimens (Figure 7; Table 2, n = 149).

The diet of the smallest size class (5-15 mm SL) is composed mainly of harpacticoid copepods. The next size class (15-20 mm SL) fed on a similar diet, although the percentage of harpacticoids taken decreased and that of polychaetes and cirripede nauplii increased. These changes were further magnified in the 20- to 25-mm size class. In the next size classes (25-50 mm), there was a change and the green alga, *Ulva* sp., contributed significantly to the diet.

Poor diving conditions in September, October, and December reduced the sample size and only nine fish in the 50- to 165-mm size range were analysed. In general, these fish showed an increasing tendency to take more amphipods, and less

TABLE 1.—Changes in the percentage composition of the food of *Diplodus sargus* with length during the period February to July 1975, as assessed by the comparative feeding index (CFI) and occurrence (Occ.) methods. In the case of the former, all values exceeding 30% have been italicized in order to emphasize those food items which contribute maximally to the diet (— = absent).

	Size classes (mm)											
	5-15		15-20		20-25		25-35		35-50		50-165	
Taxon	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.
Chlorophyta	—	—	—	—	—	—	1.3	33.3	1.0	25.0	12.8	41.7
Rhodophyta	—	—	—	—	—	—	—	—	0.2	8.3	1.6	16.7
Chrysophyta	—	—	0.2	11.8	—	—	—	—	—	—	0.3	2.8
Polychaeta	2.4	33.3	11.8	76.5	16.7	75.0	3.6	50.0	1.4	33.3	12.8	47.2
Crustacea												
Amphipoda	*47.4*	77.8	5.8	29.4	5.0	25.0	7.8	66.7	*80.1*	66.6	*58.1*	72.2
Ostracoda	0.5	22.2	4.2	58.8	1.2	75.0	0.2	16.7	0.1	8.3	—	—
Harpacticoid copepoda	*45.9*	88.9	*74.2*	82.4	*69.3*	100.0	*80.9*	66.7	1.3	25.0	0.4	11.1
Isopoda	1.2	33.3	1.0	35.3	7.4	75.0	5.0	50.0	3.3	50.0	4.2	33.3
Brachyura (zoaea)	—	—	—	—	0.1	12.5	—	—	—	—	—	—
Tanaidacea	—	—	—	—	—	—	0.1	16.7	0.1	8.3	—	—
Macrura	—	—	—	—	—	—	0.1	16.7	0.2	16.7	—	—
Mysidacea	—	—	—	—	—	—	0.2	16.7	—	—	0.1	2.8
Insecta	—	—	—	—	0.2	12.5	—	—	—	—	0.1	2.8
Mollusca	—	—	—	—	—	—	—	—	0.1	8.3	4.1	22.2
Echinodermata	—	—	—	—	—	—	—	—	—	—	0.1	2.8
Unidentifiable fragments	2.6	44.4	3.0	52.9	0.1	12.5	0.8	50.0	12.2	66.7	5.4	52.8
No. of fish examined	9		17		8		6		12		36	
Average no. of points allotted per stomach	18.8		13.4		7.3		20.3		17.2		13.2	

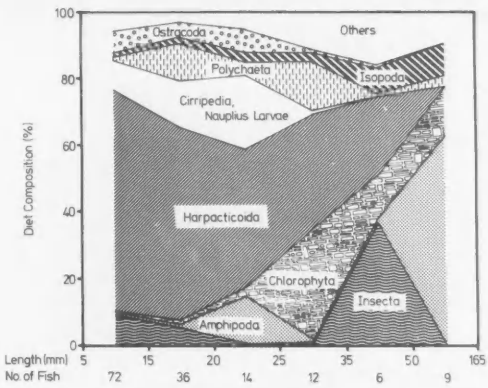

FIGURE 7.—Changes in diet with length of *Diplodus sargus*, collected between August and December 1975, as shown by the comparative feeding index. Food items included in Others are the same as for Figure 8, in addition to the unidentified trochophore larva.

algae, diatoms, chironomid larvae, and hydrozoa as they grow larger.

Identity of Food

Diatoms: two species of the genus *Licmophora*, predominantly *L. pfannkucheae*, as well as *L. ehrenbergii*.

Other algae: the chlorophytan algae of the genus *Ulva* most frequent, although some of the larger size classes also fed on *Caulerpa filiformis* (50-165 mm: 7.5% in summer and 2.9% in winter), *Bryopsis* sp., *Enteromorpha* sp., and *Valonia* sp. Some rhodophytans taken, including *Ceramium* sp., *Hypnea spicivera*, *Polysiphonia* sp., and *Tayloriella* spp.

Harpacticoid copepods: 12 species, only 4 common, identification was not possible.

Amphipods: 28 species—7 caprellid species including *Caprella danilevskii*, *C. penantis*, *C. scaura*, and *Caprellina longicollis*; *Cerapus tubularis*; *Corophium? acherusicum*, and *C.? triaenonyx*; *Cymadusa* sp.; two *Gammaropsis* species including *G. holmesi*; *Jassa* spp.; *Lysianassa ceratina*; and *L. variegata*; two *Maera* species; *Paramoera capensis*; *Parelasmopus suluensis*; two *Photis* species; *Temnophlias* sp.; *Urothoe* sp.; and three unidentified species.

Isopods: nine species—*Cymodocella pustulata*, *C. sublevis*, *Dynamenella huttoni*, *D. macrocephala*, *Exosphaeroma antikraussi*, *Gnathia* sp., *Janiropsis* sp., *Panathura* sp., and a *Stenetrium* species.

Polychaetes: *Dodecaceria pulchra*, *Eulalia trilineata*, two *Nereis* species, an *Onuphis* sp., and terebellid tentacles most commonly found in the gut contents, as well as *Pista* sp., *Pomatoleois kraussi*, and *Serpula vermicularis*.

Ostracods were not identified.

TABLE 2.—Changes in percentage composition of the food of *Diplodus sargus* with length during the period August to December 1975, as assessed by the comparative feeding index (CFI) and occurrence (Occ.) methods. In the case of the former, all values greater than 30% have been italicized in order to emphasize those food items which contribute maximally to the diet (— = absent).

	Size classes (mm)											
	5-15		15-20		20-25		25-35		35-50		50-165	
Taxon	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.
Chlorophyta	0.2	4.2	0.6	8.3	2.9	28.6	*33.4*	50.0	13.5	33.3	14.3	55.6
Rhodophyta	—	—	—	—	—	—	0.9	33.3	0.8	33.3	—	—
Chrysophyta	—	—	—	—	—	—	0.7	25.0	8.7	33.3	7.4	11.1
Hydrozoa	—	—	—	—	—	—	—	—	—	—	1.1	11.1
Polychaeta	1.1	20.8	10.4	47.2	4.0	35.7	14.7	33.3	0.9	16.7	4.0	22.2
Crustacea												
Amphipoda	0.3	6.9	1.7	27.8	14.1	57.1	2.4	25.0	6.5	50.0	*62.5*	100.0
Ostracoda	6.0	37.5	5.5	55.6	6.4	64.3	0.8	16.7	0.4	16.7	0.1	11.1
Harpacticoid copepoda	*67.8*	86.1	*58.1*	94.4	*41.6*	100.0	29.6	83.3	17.6	100.0	—	—
Isopoda	1.0	16.7	2.1	25.0	3.4	42.9	3.0	25.0	6.9	50.0	9.8	44.4
Brachyura	0.1	5.6	—	—	0.2	14.3	0.2	8.3	—	—	0.2	11.1
Cirripedia	8.8	36.1	13.9	66.7	21.5	42.9	1.3	8.3	—	—	—	—
Leptostraca	—	—	0.3	5.6	—	—	—	—	—	—	—	—
Tanaidacea	—	—	—	—	0.2	14.3	—	—	—	—	—	—
Macrura	—	—	—	—	0.7	7.1	—	—	—	—	—	—
Insecta	8.8	36.1	4.8	27.8	0.5	21.4	3.8	33.3	37.2	50.0	—	—
Mollusca	—	—	—	—	—	—	—	—	—	—	0.3	11.1
Trochophore larvae	4.6	30.6	0.3	5.6	1.6	14.3	1.2	8.3	—	—	—	—
Unidentifiable fragments	1.3	20.8	2.3	30.6	2.9	28.6	8.1	41.7	7.5	50.0	0.2	11.1
No. of fish examined	72		36		14		12		6		9	
Average no. of points allotted per stomach	13.7		17.5		20.4		12.0		14.8		18.2	

Insects: only the larva of the chironomid *Telmatogeton minor*.

Brachyurans: *Rhyncoplax bovis* and the gut of an unidentified crab (in a single case).

Molluscs: *Gibbula rosea*, *Helcion pruinosus*, *Philine aperta*, and a rhaciglossid (no shell, so not possible to identify further).

Hydrozoans: *Symplectoscyphus* sp. and *Thecocarpus formosus* were ingested by one fish in the 50- to 70-mm size class.

Echinoderms: *Parechinus* sp.

Tanaidaceans: *Leptochelia barnardi* most commonly found, also an *Apseudes* sp.

Mysidaceans: only one species, *Mysidops similis*, could be identified with any certainty.

Diplodus cervinus

The diet of *Diplodus cervinus* is illustrated in Figure 8 and Table 3 ($n = 67$). The juveniles (10-20 mm) fed mainly on harpacticoid copepods and chironomid larvae. In the next size class (20-35 mm), juveniles of the sand shrimp, *Palaemon pacificus*, were taken instead of chironomid larvae. This trend continues in the 35- to 50-mm size class, the diet being composed largely of *P. pacificus* as well as harpacticoid copepods. Polychaetes are more important in this size group, a trend which is maintained in all larger size classes. In the larger fish, there was again a changeover, the percentage of amphipods taken being 65.7% (50-75 mm) and 27.6% (75-100 mm). Unidentifiable crustacean fragments in these size classes composed 12.6% and 47.9%, respectively, which is partly explained by the fact that 6 of the 40 fish were taken at night and their stomach contents were largely digested and thus indistinguishable. The diet of the largest size class (100-135 mm) was made up mainly of polychaetes.

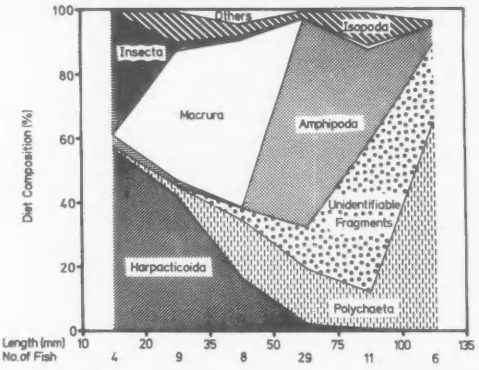

FIGURE 8.—Changes in diet with length in *Diplodus cervinus*, as shown by the comparative feeding index. Food items included in Others are: chlorophytan algae, cirripede nauplii, coralline algae, molluscs, mysidaceans, ostracods, tanaidaceans, and the unidentified trochophore larva.

Identity of Food

The diet was composed of almost all the food species listed for *D. sargus*, although in differing proportions, as well as the following: *Cymodocella eutylos* (isopod), *Littorina knysnaensis* (mollusc),

TABLE 3.—Changes in the percentage composition of the food of *Diplodus cervinus* with length, as assessed by the comparative feeding index (CFI) and occurrence (Occ.) methods. In the case of the latter, all values exceeding 30% have been italicized in order to emphasize those food items which contribute maximally to the diet (— = absent).

	Size classes (mm)											
	10-20		20-35		35-50		50-75		75-100		100-135	
Taxon	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.
Chlorophyta	—	—	—	—	4.6	12.5	—	—	—	—	—	—
Rhodophyta	—	—	—	—	—	—	—	—	—	—	1.9	16.7
Polychaeta	0.2	25.0	3.8	33.3	17.6	50.0	17.2	72.4	11.4	18.0	*65.4*	82.3
Crustacea												
Amphipoda	4.1	25.0	1.0	33.3	0.4	25.0	*65.7*	74.9	27.6	45.0	5.8	33.3
Ostracoda	—	—	0.2	22.2	—	—	—	—	0.6	9.0	—	—
Harpacticoid copepoda	*56.5*	100.0	*41.6*	77.8	16.5	87.5	2.2	51.7	0.1	9.0	—	—
Isopoda	—	—	10.0	44.4	4.2	25.0	1.5	20.7	11.0	27.0	1.7	16.7
Cirripedia (nauplii)	—	—	—	—	—	—	0.5	6.9	—	—	—	—
Macrura	—	—	*41.2*	44.4	*53.2*	50.0	—	—	1.0	9.0	—	—
Tanaidacea	—	—	—	—	—	—	0.2	6.8	—	—	—	—
Mysidacea	—	—	—	—	—	—	0.1	3.4	—	—	—	—
Insecta	*39.0*	50.0	2.2	55.6	0.4	12.5	—	—	—	—	—	—
Mollusca	—	—	—	—	—	—	—	—	0.4	9.0	1.9	16.7
Trochophore larvae	0.2	25.0	—	—	—	—	—	—	—	—	—	—
Unidentifiable fragments	—	—	—	—	3.1	50.0	12.6	79.3	*47.9*	36.0	23.3	33.3
No. of fish examined	4		9		8		29		11		6	
Average no. of points allotted per stomach	8.3		19.3		8.0		10.0		6.4		11.1	

Phoxostoma sp. (amphipod), and *Corallina* sp. (rhodophytan alga).

Sarpa salpa

The percentage composition of the diet of *Sarpa salpa* is illustrated in Figure 9 and Table 4. The food habits of this species changed from being primarily a carnivore as a juvenile to a herbivore as a subadult.

Juveniles in the 10- to 25-mm size classes fed mainly on harpacticoid copepods. In the next size class (25-35 mm), however, the total animal contribution is only 15.1%, diatoms and rhodophytan algae being most important. Diatoms are taken in decreasing amounts from then on and those fish >75 mm SL fed predominantly on chlorophytan and rhodophytan algae.

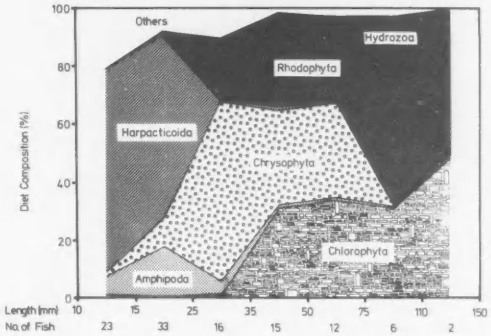

FIGURE 9.—Changes in diet with length of *Sarpa salpa*, as shown by the comparative feeding index. Food items included in Others are: bryozoans, cirripede nauplii, crab zoaea, fish muscle, insects, isopods, leptostracans, mysidaceans, ostracods, polychaetes, rhaciglossid molluscs, and tanaidaceans.

Identity of Food

Chlorophytan algae: eight species—*Bryopsis* sp., *Caulerpa filiformis*, *Chaemaedoris delphini*, *Cladophora* spp., *Enteromorpha* sp., *Rhizoclonium* sp., and *Ulva* sp.

Rhodophytan algae: *Ceramium* sp., *Champia compressa*, *Hypnea spicifera*, *Polysiphonia* sp., and *Tayloriella* sp. commonly taken as well as *Acrosorium* sp., *Arthrocardia* sp., *Centroceras* sp., *Corallina* spp., *Polyzonia elegans*, and *Pterosiphonia cloiophylla*.

Chrysophytan algae: three species of diatoms—*Isthmia enervis*, *Licmophora ehrenbergii*, and *L. pfannkucheae*.

Hydrozoans: *Gattya humilis* commonly ingested by the 75- to 100-mm size class, whereas *Sertularella* sp. and *Thecocarpus formosus* were uncommon.

Polychaetes: only two species of *Nereis*.

Isopods: uncommon, but six species were found—*Dynamenella huttoni*, *D. macrocephala*, *Gnathia* sp., *Janiropsis* sp., *Panathura* sp., and *Stenetrium* sp.

TABLE 4.—Changes in the percentage composition of the food of *Sarpa salpa* with length, as assessed by the comparative feeding index (CFI) and occurrence (Occ.) methods. In the case of the latter, all values exceeding 30% have been italicized in order to emphasize those food items which contribute maximally to the diet (— = absent).

	Size classes (mm)													
	10-15		15-25		25-35		35-50		50-75		75-100		125-150	
Taxon	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.	CFI	Occ.
Chlorophyta	0.3	8.7	—	—	0.9	31.3	*31.2*	92.0	*34.0*	91.7	*30.6*	100.0	*48.3*	100.0
Rhodophyta	—	—	0.4	9.1	21.3	62.5	*32.3*	76.0	28.6	66.7	*45.9*	83.3	*50.1*	100.0
Chrysophyta	0.2	8.7	9.3	24.2	*62.7*	100.0	*32.4*	68.0	*33.4*	66.7	—	—	—	—
Hydrozoa	—	—	—	—	—	—	—	—	0.1	16.7	20.5	50.0	0.8	50.0
Polychaeta	5.1	17.4	2.6	30.3	—	—	—	—	0.4	8.3	0.1	16.7	—	—
Crustacea														
Isopoda	1.7	17.4	0.9	30.3	0.1	6.3	—	—	—	—	—	—	—	—
Amphipoda	7.3	30.4	17.8	63.6	4.2	50.0	0.9	16.0	0.1	16.7	0.3	33.3	0.8	50.0
Ostracoda	6.7	26.1	1.4	36.4	0.1	6.3	0.1	12.0	—	—	—	—	—	—
Harpacticoid copepoda	*71.0*	87.0	*64.5*	72.7	0.5	18.8	1.4	24.0	—	—	—	—	—	—
Cirripedia (nauplii)	5.5	22.0	2.1	18.2	—	—	—	—	—	—	—	—	—	—
Brachyura (zoaea)	—	—	0.1	3.0	0.1	12.5	—	—	—	—	—	—	—	—
Leptostraca	0.1	4.4	—	—	—	—	—	—	—	—	—	—	—	—
Insecta	0.1	4.4	0.2	3.0	0.1	12.5	—	—	—	—	—	—	—	—
Bryozoa	—	—	—	—	—	—	—	—	—	—	0.1	16.7	—	—
Mollusca	—	—	—	—	—	—	—	—	—	—	0.1	16.7	—	—
Pisces	—	—	—	—	0.2	6.3	—	—	—	—	—	—	—	—
Unidentified fragments and sand	2.0	26.1	0.7	24.2	9.8	31.3	1.7	32.0	3.4	41.7	2.4	50.0	—	—
No. of fish examined	23		33		16		25		12		6		2	
Average no. of points allotted per stomach	7.8		9.5		13.8		15.7		16.5		15.5		28.0	

Amphipods: also uncommon except in juveniles which took the following 15 species: *Caprella cicur* and two other species of *Caprella*, *Cerapus* sp., *Corophium* sp., *Gammaropsis* sp., *Lysianassa ceratina*, *L. variegata*, *Jassa* sp., *Maera* sp., *Paramoera capensis*, *Parelasmopus suluensis*, *Photis* sp., and two unidentified species.

Harpacticoid copepods: eight species.

Insects: larvae of the chironomid *Telmatogeton minor*.

Tanaidaceans: *Leptochelia barnardi*, uncommon.

Molluscs: rhaciglossid.

DENTITION AND GUT MORPHOLOGY

Diplodus cervinus—there are six upper and four lower incisors which are narrower than those of *D. sargus*, and there are fewer molars, the number increasing with age (Figure 10A). This would indicate that adult *D. cervinus* feed on softer foods than *D. sargus*, which is borne out as the diet of the former consists primarily of polychaetes, whereas the latter took amphipods and molluscs as well. The gut of *D. cervinus* is short with a G/S ratio of 0.7 in a 16.5-mm fish and 0.95 in one 74 mm long.

Diplodus sargus—there are four stout incisors and three to four rows of fairly large molars in each jaw (Figure 10B), the latter increasing in size and number with age. The teeth are those of a typical omnivore (Weatherly 1972). The G/S ratio was 0.76 in a 16.5-mm fish and this is within the range of omnivores as defined by Nikolsky (1963).

Sarpa salpa—this species shows a change in dentition correlated with age and diet. The young fish are carnivorous and have short, pointed coni-

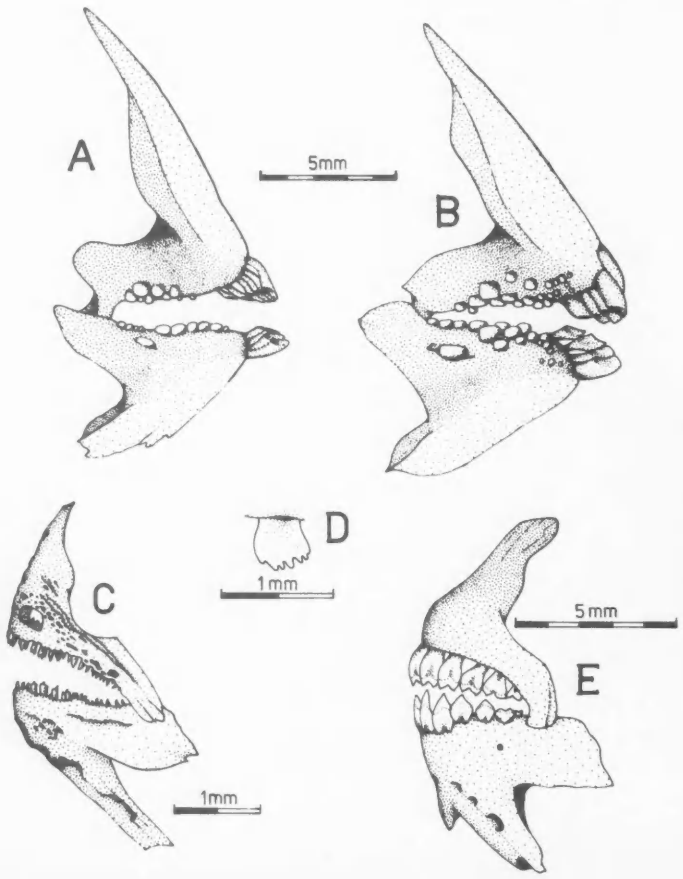

FIGURE 10.—Dentition. A. Medial view of the left upper and lower jaws of *Diplodus cervinus* (MSC 75-36, 94 mm SL). B. Medial view of the left upper and lower jaws of *D. sargus* (MSC 75-34, 107 mm SL). C. Lateral view of the upper and lower jaws of a juvenile *Sarpa salpa* (MSC 75-39, 20 mm SL). D. Lateral view of a single tooth of a subadult *S. salpa* (MSC 75-37, 39 mm SL). E. Lateral view of the upper and lower jaws of an adult *S. salpa* (RUSI 74-323, 99 mm SL).

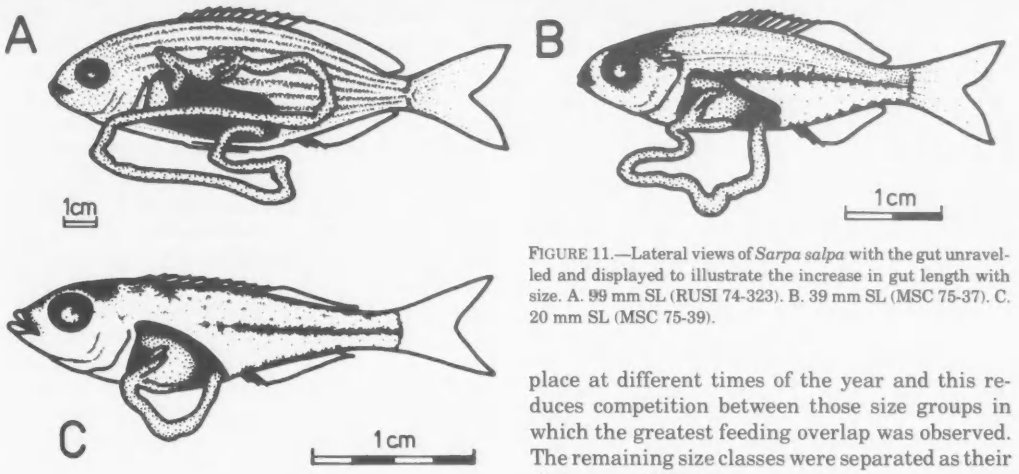

FIGURE 11.—Lateral views of *Sarpa salpa* with the gut unravelled and displayed to illustrate the increase in gut length with size. A. 99 mm SL (RUSI 74-323). B. 39 mm SL (MSC 75-37). C. 20 mm SL (MSC 75-39).

cal teeth to grasp prey (Figure 10C). Multicusped, incisiform teeth begin to break through when the fish are about 20 mm long (Figure 10D). The pointed teeth are completely replaced by the time the fish are 35 mm long, after which they feed predominantly on algae (approximately 60% CFI). The multiple cusps wear away and the teeth are bicuspid incisiform by the time the fish are 65 to 75 mm long (Figure 10E). These can nip at algae and the diet is composed of 65 to 77% plant matter at this stage.

The gut shows a corresponding change in length with diet, a long gut being characteristic of a herbivore. The G/S ratio increases from 0.86 in a 20-mm fish (Figure 11C, typically omnivorous) to 1.36 in a 39-mm fish (Figure 11B), and 2.66 in a 99-mm individual (Figure 11A). This latter value is typical of a herbivore (Nikolsky 1963), although not as pronounced as in some other herbivorous fish species.

DISCUSSION

A number of fish species occur as juveniles or spend their entire life cycle in the eastern Cape intertidal (see description under Study Area). The family Sparidae includes the largest number and the present investigation of the trophic relationships of three of these was initiated as competitive interaction is often most vigorous in closely related fish (Fryer and Iles 1972). There is an intense dietary overlap in some cases and the available resources are subdivided in two main ways. Recruitment of juveniles of the three species takes place at different times of the year and this reduces competition between those size groups in which the greatest feeding overlap was observed. The remaining size classes were separated as their diets were different.

Small juveniles of the three species have the most similar diets of all size classes studied. The resulting competition is reduced by two mechanisms. Firstly, juveniles of *Sarpa salpa* occur in the tide pools primarily from July to September (Figure 5) whereas those of *Diplodus cervinus* were found during October and November (Figure 4) and *D. sargus* was present throughout the year (Figure 3). Secondly, at the time of maximal competition (July-November), the diet of small *D. sargus* includes food items not taken at other times of the year, e.g., chironomid larvae and cirripede nauplii (Figure 7). This may be due to either the presence of these prey items only at that time of the year and/or to the effects of competition forcing *D. sargus* to include them in its diet. A combination of both factors would appear to be operative in the case of the chironomids as the larvae were obtained in bottom samples taken in October-November and not in March. No data are available for cirripede nauplii, crab zoaea, and the unidentified trochophore larva as plankton samples were not taken.

Competition for food is greatly reduced by the time the three sparids are about 25 to 30 mm long. At this stage, *S. salpa* feeds mainly on diatoms and red algae (Figure 9); *D. cervinus* ingests *Palaemon pacificus*, harpacticoid copepods, and isopods (Figure 8); and *D. sargus* takes green algae, harpacticoids, chironomid larvae, and cirripede nauplii (Figures 6, 7). The separation is equally distinct in subadult fish as *S. salpa* is then a herbivore, *D. cervinus* takes polychaetes, some amphipods, and isopods, while *D. sargus* feeds on amphipods and

green algae. The overlap on amphipods by the latter two species may be partially compensated for by behavioral separation. *Diplodus cervinus* is a secretive substrate feeder whereas *D. sargus* is a more open water fish tending to feed on vertical rock surfaces away from the bottom. The fact that neither species was very common intertidally in these size classes may also contribute towards a reduction in competition.

The diet of large juvenile *S. salpa* is unusual in that it consists mainly of diatoms and epiphytic rhodophytan algae which occur commonly on corallines, *Hypnea spicifera* and *Tayloriella* spp. (M. H. Giffen, pers. commun.). The fish must, therefore, selectively separate these food items as few fragments of the algae on which they grow were found in the stomach contents. This is in contrast to *Rhabdosargus holubi*, also a sparid, which ingests algae for their epiphytic diatoms rather than separating them, even though the algae are not digested (Blaber 1974). The situation may be similar to this in larger *S. salpa* as the rectal contents appeared to be relatively undigested and fewer diatoms were observed on the algae (Figure 12).

Temporal separation of juveniles to reduce competition has not been reported previously for tide pool fish species as far as I am aware, although it has been observed in two pelagic plankton feeders from the Adriatic, the anchovy and sardine (Vučetič 1975). Large dietary overlaps have been noted in several intertidal fish, including blennies, clinids, gobies, and labrids (Gibson 1968, 1972). These fed predominantly on crustaceans and it is possible that similar mechanisms reduce competitive pressure amongst them, although this was not determined as samples were only taken for 2 mo.

The data presented indicates that *D. cervinus* is a carnivore, *D. sargus* is an omnivore, and *S. salpa* an omnivore when juvenile and a herbivore when adult. Similar feeding habits were found for adults of the same three species in the Klein River estuary (Talbot 1954). The dentition and gross gut morphology changed with size and this was most marked in *S. salpa*, corresponding with the observed diet. Comparable transformations have been reported for other fish species (Nikolsky 1963).

Two other sparids, *Sparodon durbanensis* and *R. holubi*, cohabit with those studied in the littoral zone. The few specimens examined had fed mainly on harpacticoid copepods as small juveniles, with a resultant overlap with *D. sargus* as all three occurred in the research area in November-December. Large specimens were not examined, but *R. holubi* appears to be an omnivore as a juvenile in estuaries and a carnivore feeding on molluscs as an adult (Talbot 1954; Blaber 1974). Adult *S. durbanensis* are carnivores feeding on small fish, molluscs, and crustaceans (Biden

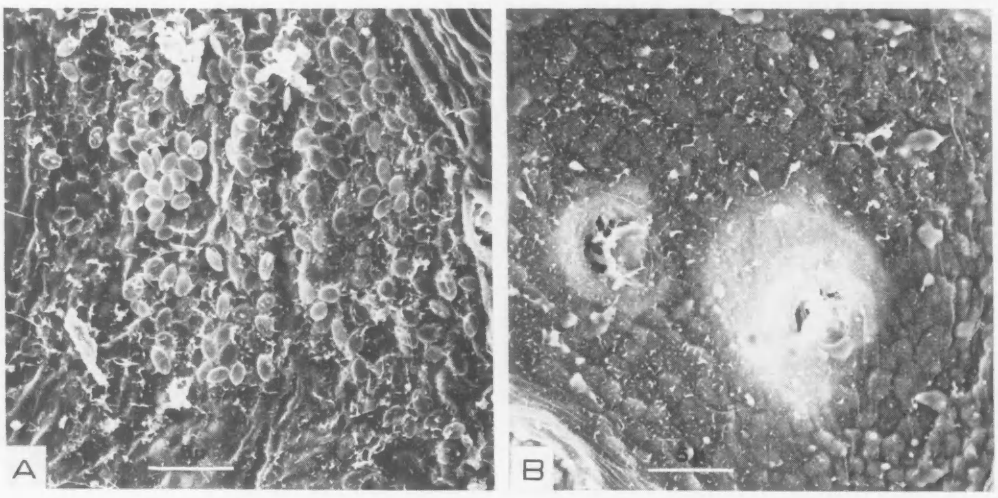

FIGURE 12.—Scanning electron micrograph of the surface of a chlorophytan alga, *Ulva* sp., removed from the gut of *Sarpa salpa* (147 mm SL) to show the disappearance of diatoms. A. Oesophageal sample. B. Rectal sample.

1954). Competitive pressure is, therefore, minimized between the five sparid fish species commonly occurring in the littoral zone.

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EFFECT OF STARVATION ON THE HISTOLOGICAL AND MORPHOLOGICAL CHARACTERISTICS OF JACK MACKEREL, *TRACHURUS SYMMETRICUS*, LARVAE

GAIL H. THEILACKER[1]

ABSTRACT

Histological and morphological criteria were developed to assess the nutritional condition of laboratory-reared jack mackerel, *Trachurus symmetricus*, larvae. A comparison of the histological features of fed and starved larvae revealed that the digestive tract and its associated glands were the first tissues to be affected by starvation. The extent of cellular deterioration increased with time of starvation. To classify larval condition, histological characteristics of the pancreas and gut were given numerical grades. The histological technique correctly classified 83% of the feeding and starving larvae.

The morphometric analysis relied upon a stepwise discriminant analysis that used a combination of five measurements (standard length, head length, eye diameter, body depth at the pectoral, and body depth at the anus) to estimate individual larval condition. The morphometric method was as sensitive as the histological examination in determining whether or not a larva was fed or starved. Ultimately, these histological and morphological criteria may be useful for estimating larval survival in the field by assessing the condition of sea-caught larvae.

Fishery scientists generally agree that observed fluctuations in recruitment of young fish to a fish stock may be the consequence of mortality during the larval stage. Because starvation is probably one of the principal causes of mortality (Hunter 1976a), a need exists to develop criteria for detecting the incidence of starvation in sea-caught specimens. Several scientists have suggested that the differences in body form between feeding and starving larvae could be used to identify the nutritional status of larvae caught in sea surveys. For example, Shelbourne (1957) based his assessment of the condition of ocean-caught plaice, *Pleuronectes platessa*, larvae on their external appearance. Certain morphometric measurements also can be indicative of starvation. A decrease in thickness of the larval fish body has been correlated with starvation for several marine and freshwater fish larvae [herring, *Clupea harengus*, and plaice (Ehrlich et al. 1976); northern anchovy, *Engraulis mordax* (Arthur 1976); anchovy, *E. japonica* (Honjo et al. 1959; Nakai et al. 1969); pike, *Esox lucius*, and carp, *Cyprinus carpio* (Kostomarova 1962)]. Other morphological features (Ehrlich et al. 1976) considered to be indicative of starvation in herring and plaice were a decrease in the angle of the pectoral girdle, a change in the ratio of the head to eye height (herring only), and a decrease in the relative condition factor. Coincident with morphometric differences caused by starvation, Ehrlich et al. (1976) described histological changes in the gut and liver. The histological approach was used to classify yellowtail, *Seriola quinqueradiata*, larvae into "feeding," "semi-feeding," and "starving" groups by Umeda and Ochiai (1975). This technique was also effective for diagnosing starvation in northern anchovy larvae (O'Connell 1976). In both species, degeneration of cells of digestive organs was the best indicator for identification of starvation. Several other studies also have correlated starvation in fish larvae with degeneration of the digestive organs, mainly the gut. Kostomarova (1962) described a retardation in development of the gut in larvae of starved carp and pike and a reduction in the depth of the epithelial cells lining the gut. Reduced gut cell height was also reported for the larvae of starved yellowtail (Umeda and Ochiai 1975), herring, and plaice (Ehrlich et al. 1976).

Morphological criteria are preferable to histological ones because they take much less time to determine and require no special preservation techniques. However, histological criteria may be more accurate for classifying individual larva.

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The purpose of this study was to develop morphological and histological criteria for assessing the nutritional condition of jack mackerel larvae and to evaluate these criteria by comparing their success in identifying fed and starved larvae reared in the laboratory. Ultimately, criteria based on these results may be useful for estimating larval survival in the field by assessing the condition of sea-caught larvae.

MATERIALS AND METHODS

Jack mackerel eggs were collected by towing a 1-m (mouth diameter, 0.505-mm mesh) plankton net just below the sea surface at various locations between 20 and 200 mi (32 and 320 km) off the coast of southern California in June and July 1975 and in May 1976. The eggs were separated from most of the plankton at sea and then sorted by developmental stage at the Southwest Fisheries Center, La Jolla, Calif. Temperature was maintained at 15°C during sorting and in the larval rearing containers. The light cycle was 12 h light and 12 h dark. Five hundred normally developing eggs from a single day's spawning were transferred into 100 l black Kydex[2] circular rearing tanks containing filtered seawater (5μm, Cuno filtered). There were three experiments and two treatments in each experiment; larvae in one tank were offered food while those in the other were not. The fed larvae were given a diet of a naked dinoflagellate, *Gymnodinium splendens* (50/ml), a rotifer, *Brachionus plicatilis* (30-40/ml), and a copepod, *Tisbe* sp. (1 or 2/ml). This feeding method has been described (Lasker et al. 1970; Theilacker and McMaster 1971; Hunter 1976b).

Histological criteria were developed in the first two experiments. The sampling procedure and the number of larvae sampled differed depending on the requirements of the analysis. Collectively, a total of 152 larvae were examined. In the third experiment, usually 15 larvae were sampled daily for 5 days from the "fed" tank (n = 69) and 3 days in the "starved" tank (n = 48). All larvae were examined both histologically and morphologically. No dead larvae were sampled because the postmortem change which takes place in tissues of fish larvae, due to digestion by their own enzymes (autolysis), resembled antemortem destruction caused by starvation. Standard length of each larva was measured on a slide; then seawater was removed and replaced by Bouin's fixative. Preserving individual larvae in this manner assured that each would be straight and flat, facilitating subsequent morphometric measurements. Five measurements were taken after preservation to monitor daily changes in larval body form and determine effects of starvation: standard length (SL, tip of upper jaw to tip of notochord), head length (HL, tip of upper jaw to cleithrum), eye diameter (ed), body depth at the pectoral (bd-1), and body depth at the anus (bd-2). Standard length shrinkage in Bouin's fixative was 11.5%. Next, measured larvae were prepared for histological examination using standard techniques. Larvae were transferred from Bouin's to 70% ethyl alcohol after 24 h, dehydrated with an ethyl n-butyl alcohol series in a Fisher Tissuemation, and embedded in Paraplast-plus. The Paraplast paraffin blocks were frozen with fluorocarbon spray (Cryokwick) just before the larvae were serially sectioned at 5 μm in a sagittal plane. The mounted sections were stained with Harris' hematoxylin and eosin and mounted in synthetic resin.

Histological Grading System

Recently O'Connell (1976) developed a numerical, histological grading system to characterize the nutritional condition of individual northern anchovy larvae. He examined tissues of the larvae microscopically to determine the features of tissue microstructure that were affected by starvation. A grade was assigned to each feature based on the degree of similarity or dissimilarity of the histological microstructure between the starved larvae and fed larvae. I followed this method and modified it as necessary for the tissues of jack mackerel.

Each of the histological characteristics used to assess starvation in jack mackerel larvae was evaluated and assigned a grade. A grade of "3" was given to a characteristic which resembled that in "normal or healthy" larvae, a grade of "2" was given to an intermediate condition, a grade of "1" to the starved condition. Since these criteria were established by comparing actively feeding, seemingly healthy larvae with moribund larvae, it was assumed that an average of the 12 graded features examined for each larva classified the larva into the correct nutritional group: "healthy group," average grade = 2.34 to 3.00; "intermediate group" = 1.67 to 2.33; and "starved" = 1.00 to

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

1.66 (the break points establish three equal groups).

Data Analysis

In the main, conclusions are based on the results of a stepwise discriminant analysis (SWDA). A discriminant analysis allows one to distinguish between two or more groups, given a set of variables that describe the characteristics in which the individuals in each group are expected to differ. In the stepwise discriminant analysis, all the variables are introduced into a SWDA computer program and the best set of variables, based on the generalized Mahalanobis distance (Rao 1952), is selected. The first variable chosen will usually be the one which gives the best score when classifying the individuals into their predetermined groups. The score is equal to the number correctly classified. The selection of each succeeding variable improves the score until a subset is chosen which is as good as the full set of variables for discriminating the groups. All variables not included in the final subset are considered superfluous, or not necessary for classification.

RESULTS

Histological

The histological condition of yolk-sac and actively feeding larvae ("normal") was compared with that of 3-day starved larvae and many differences were noted in the cells, tissues, and organs. The degree of apparent histological deterioration of 1- and 2-day starved larvae was intermediate between the "normal" and moribund status. This condition was termed "semi-starved" by Umeda and Ochiai (1975) and "intermediate" by O'Connell (1976).

The following section describes the normal histology of actively feeding jack mackerel larvae and that of starving larvae. Twelve histological criteria, which appeared to be indicators of starvation, were identified; they are numbered in the test below and are referenced in the photomicrographs (Figures 1-12).

Brain (Figures 3, 4)

The primitive brain cells exhibited a high incidence of mitotic activity (1) in normal larvae and there was relatively little intercellular space (2) between the round cells. In starved larvae, mitotic activity was arrested and many of the cells were shrunken, which caused large clear areas to appear between densely stained, atrophied cells.

Liver (Figures 5-8)

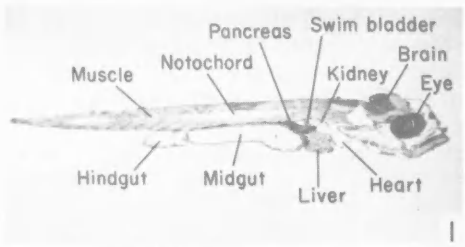
In the normal larval jack mackerel liver the hepatic cords were two cells thick. Within each hepatocyte, the nucleus (3) was regular in shape and distinct. The cytoplasm (4) was well dispersed with intracellular spaces, probably an area where glycogen and lipid are stored. Sinusoid areas, where metabolic exchanges take place between the hepatic cords, contained blood cells. After starvation for a few days, the liver atrophied, the cytoplasm condensed, stained darkly, and intracellular spaces had disappeared. There were focal degenerative or necrotic areas and accumulations of eosinophilic granules and masses. Nuclei were often irregular in shape and granules appeared around their periphery; these darkened areas are presumed to be condensed, inactive chromatin (Stein et al. 1975). The gallbladder (5) in starved larvae was always enlarged; normally it discharges its contents under the stimulus of food (Love 1970).

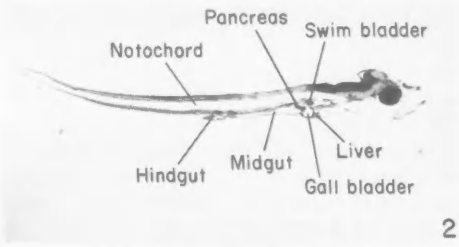
Pancreas (Figures 5-8)

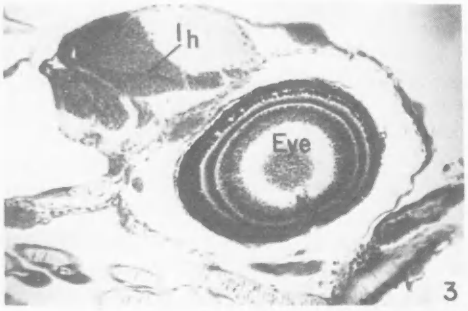
Cells of the exocrine pancreas were arranged in series, in a circular fashion, as a secretory unit called an acinus. The nucleus (6), clear and distinct, was located in the basal portion of the pyramidal cells. The acinar arrangement of the pancreatic cells (7) was found to be very sensitive to deprivation of food. A breakdown in the symmetry in the acinus was slight but usually detectable after 1 day of starvation. Tissue degeneration after 3 days of starvation was extreme. The nucleus was irregular and uniformly stained and there was no detectable acinar arrangement. The presence of zymogen, digestive proenzyme secreted by the acinus and stored as granules at its central apex, was usually associated with starvation.

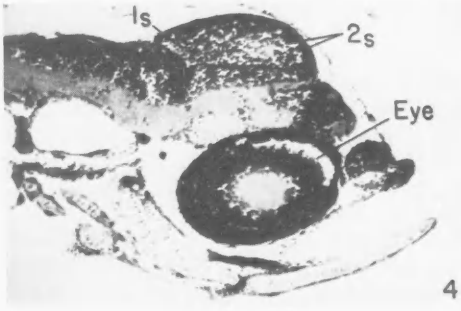
Digestive Tract (Figures 7-12)

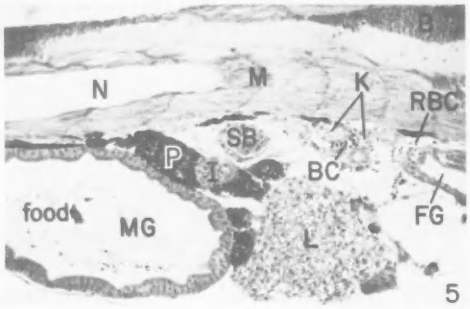
The columnar epithelial cells of the midgut were closely united (8) in a single layer. Microvilli were visible along the border of the lumen giving a brush effect. In starved larvae, the midgut cells











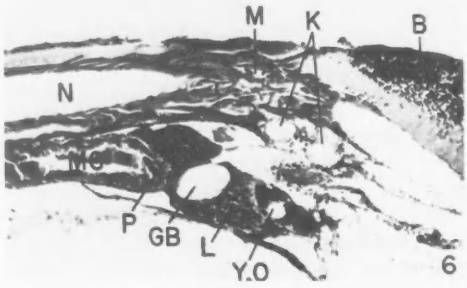


FIGURE 1.—*Trachurus symmetricus* larva, day 8, fed for 3 days. All 12 histological criteria graded as "healthy." 32 ×.

FIGURE 2.—*Trachurus symmetricus* larva, day 8, starved for 3 days. All 12 histological criteria graded as "starved." 32 ×.

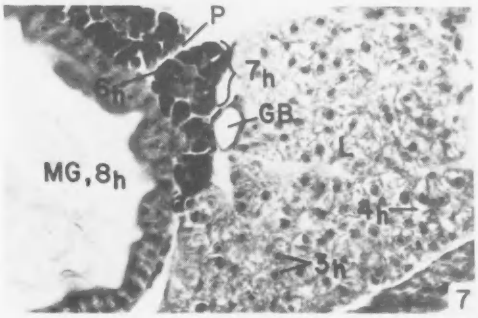
FIGURE 3.—Head of fed larva, graded "healthy." Mitotic activity (1 h) is indicated. Note close proximity of primitive brain cells to each other. 200 ×. h = histological grade = healthy.

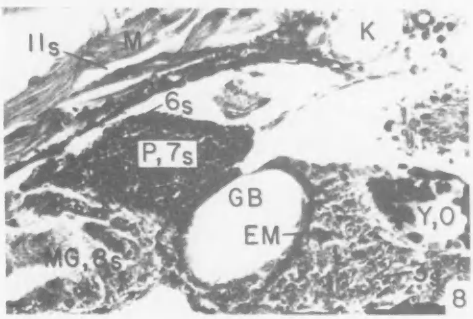
FIGURE 4.—Head of starved larva, graded "starved." Atrophied and darkly stained primitive brain cells (1 s); large intercellular spaces (2 s). 200 ×. s = histological grade = starved.

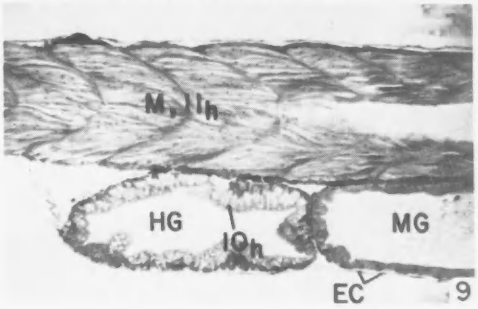
FIGURE 5.—Day 8 fed larva. Histological features graded "healthy." 200 ×. See enlargement, Figure 7. B = brain, BC = blood cells (white or immature red), FG = foregut, I = Islet of Langerhans (endocrine pancreas), K = kidney, L = liver, MG = midgut, M = muscle, N = notochord, P = exocrine pancreas, RBC = red blood cells, SB = swim bladder.

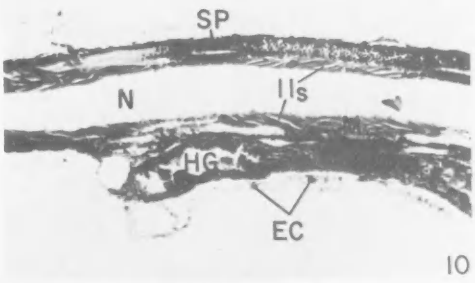
FIGURE 6.—Day 8, starved larva. Histological features graded "starved." 200 ×. See enlarge, Figure 8. GB = gallbladder, O = oil, Y = yolk, see Figure legend 5 for rest of symbols.

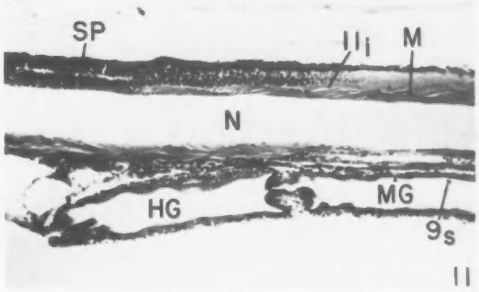
FIGURE 7.—Day 8 fed *Trachurus symmetricus* larva. Enlargement of Figure 5. Midgut cells in close union (8 h); prominent nuclei (3 h) and large intracellular spaces (4 h) in the liver; pancreatic nuclei distinct (6 h) and cells arranged in a circular unit (acinus) (7 h); gallbladder (GB) "normal." 480 ×. h = histological grade = "healthy," L = liver, MG = midgut, P = exocrine pancreas.











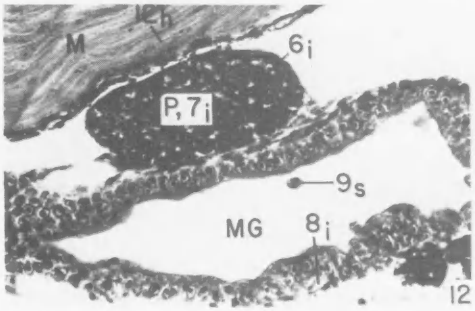


FIGURE 8.—Day 8, starved *Trachurus symmetricus* larva. Enlargement of Figure 6. Loss of integrity of midgut cells (8 s); atrophied liver with dark staining and irregular nuclei (3 s); no acinar cellular arrangement in pancreas (7 s); separated muscle fibers (11 s); swollen kidney (K); distended gallbladder (GB); note presence of yolk and oil (Y, O), and eosinophilic mass (EM) in liver. 480 ×. s = histological grade = "starved," M = muscle, MG = midgut, P = exocrine pancreas.

FIGURE 9.—Day 8 fed larva. Large eosinophilic inclusions in hindgut (10 h); muscle fibers closely packed (11 h); thin, epithelial integumental cells (EC) are prominent below gut and above trunk musculature. 200 ×. h = histological grade ="healthy," HG = hindgut, M = muscle, MG = midgut.

FIGURE 10.—Day 8, starved larva.Loss of cellular structure in hindgut; enlarged epithelial integument cells (EC); separated muscle fibers (11 s). 200 ×. s = histological grade = "starved," HG = hindgut, M = muscle, N = notochord, SP = spinal cord.

FIGURE 11.—Day 7 larva, starved 2 days and histologically graded "intermediate." No inclusions in hindgut; cellular separation in midgut (MG) and hindgut (HG); midgut cells sloughing (9 s); muscle fibers beginning to separate (11 i). 200 ×. i = histological grade = intermediate, s = histological grade = "starved," M = muscle, N = notochord, SP = spinal cord.

FIGURE 12.—Day 7 larva, starved 2 days, graded "intermediate." Abundant intermuscular tissue (12 h); no muscle (M) fiber separation; pancreatic nuclei (6 i) not distinct and cellular acinar arrangement lacking (7 i); midgut cells separating (8 i) and sloughing (9 s). 480 ×. i = histological grade = intermediate, s = histological grade = "starved," MG = midgut, P = exocrine pancreas.

began to separate from each other. It appeared that the midgut was extremely vulnerable to a deficiency of food and usually after 1 day of starvation, single mucosal cells could be seen sloughed (9) into the lumen. The margin of the lumen continued to lose its integrity as starvation advanced. Cells of the hindgut of feeding larvae exhibited an accumulation of eosin staining inclusions. The inclusion bodies, which may be the sites of intracellular digestion, have been observed in other marine and freshwater fish (Kostomarova 1962; Iwai and Tanaka 1968a, b; Iwai 1968; Umeda and Ochiai 1975; O'Connell 1976). The amount, size, and intensity of the staining (10) of these inclusions varied in feeding larvae. They were not present in starving larvae.

Musculature (Figures 9, 10, 12)

In feeding jack mackerel larvae, individual muscle fibers were close together (11); they were composed of closely packed, striated, and parallel myofibrils. After a period of starvation, the fibers separated, the fibrils were not distinct, and occasionally they lost their parallel structure. Between some fibers there was a granular, basophilic, nucleated substance called "intermuscular tissue" (12) by O'Connell (1976). In starved larvae, this tissue was usually absent.

General Histological Characteristics

After jack mackerel larvae had starved for 3 days, signs of depletion were widespread. In addition to changes in major tissues and organs there was a general atrophy and disintegration of all cells and tissues including those of cartilage, kidney, endocrine pancreas, and swim bladder. The number of pyknotic nuclei (i.e., darkening and shrinking nuclei, which give the first indication that a cell is dying) increased in all tissues (see eye and brain, Figure 4). Epithelial cells of the integument were hypertrophic, twice as large as normal in 3-day starved larvae (Figure 10), and kidney tubules were swollen (Figure 6). There was always a larger yolk reserve retained by starving larvae (Figure 6). A decrease in yolk absorption in starving larvae was also reported by Kostomarova (1962) for pike and carp and by Umeda and Ochiai (1975) for yellowtail.

Histological Grading

To determine whether the classification of a jack mackerel larva required the grading of all histological features or a lesser number, a group of 27 larvae, 14 feeding and 13 starving, was examined and the resulting grades for each criterion were submitted to a SWDA. The experimental treatment (fed or starved) was unknown until after all larvae were microscopically examined. The larvae were 7 days old and had been feeding or starving for 2 days. The grading system classified all fed larvae (n = 14) into the healthy group (individual average grade of the 12 histological features ranged between 2.42 and 2.92). The average grades for the 2-day starved larvae were more variable. The larvae were classified, about equally, into each of the three nutritional groups: four had a grade range between 2.35 and 2.54, ranking in the healthy group; four were classified as intermediate, grade range 2.08 to 2.31; and five larvae were ranked as starved with the average grades ranging between 1.15 and 1.54.

Results of the SWDA on the above data disclosed that grading only two histological characteristics, the arrangement of the cells in the pancreas (variable 7) and the sloughing of mucosal cells from the midgut (variable 9), gave the same conclusions as using all 12 features. Therefore, in all subsequent histological assessments, the average grade of these two criteria, variables 7 and 9, was used as the index of larval condition.

Morphological

The jack mackerel larvae were 2.45 mm SL (preserved) at hatching and initiated feeding at 3.35 mm, 5 or 6 days after hatching (hatching = day 0, Figure 13A). At the time of first feeding, some yolk and oil were present but the yolk sac was not discernible. The relationship between the five morphological characteristics, measured to determine the effects of starvation, and days of starvation is illustrated in Figure 13B-F. Since no data have been published on the daily growth rate of field-caught jack mackerel larvae, I used length as an estimate of age. When the morphometric measurements were plotted against length, no single measurement was a reliable index of starvation, as illustrated by pectoral body depth plotted for fed and starved larvae (Figure 14). However, some limits can be set from this graph: 1) all larvae <3.30 mm SL that do not have a yolk sac probably are starving (feeding is initiated at 3.35 mm); and 2) larvae with a body depth >0.47 mm are feeding. This leaves the size class between 3.30 and 3.55 mm where the cases cannot be separated. Most individuals in this class (29 fed and 24

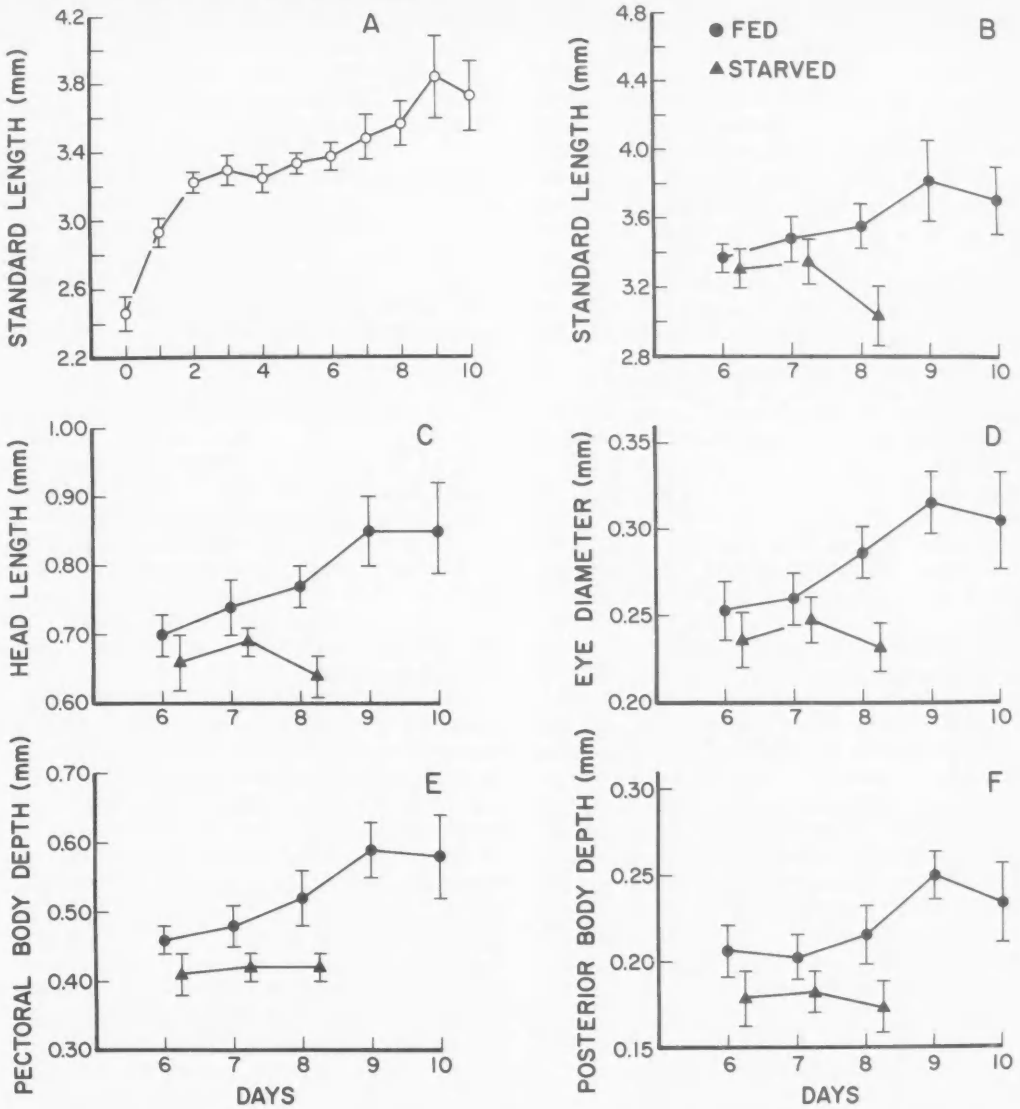


FIGURE 13.—A. Growth of *Trachurus symmetricus* larvae, with means and standard deviations. Sample size on any day was usually 15. B-F. Relationship between five morphological characteristics of *T. symmetricus* larvae and days of starvation, with means and standard deviations. Sample size was usually 15.

starved) have been feeding or starving for 1 or 2 days.

To determine whether a set of several morphometric variables could predict the condition of larvae in the 3.30 to 3.55 mm size class, a SWDA was run. Eleven morphometric variables, in which the two predetermined groups (fed and starved) were expected to differ, were entered into the SWDA: 1) HL, 2) ed, 3) bd-1, 4) bd-2, 5) HL/SL, 6) ed/SL, 7) bd-1/SL, 8) bd-2/SL, 9) ed/HL, 10) bd-1/

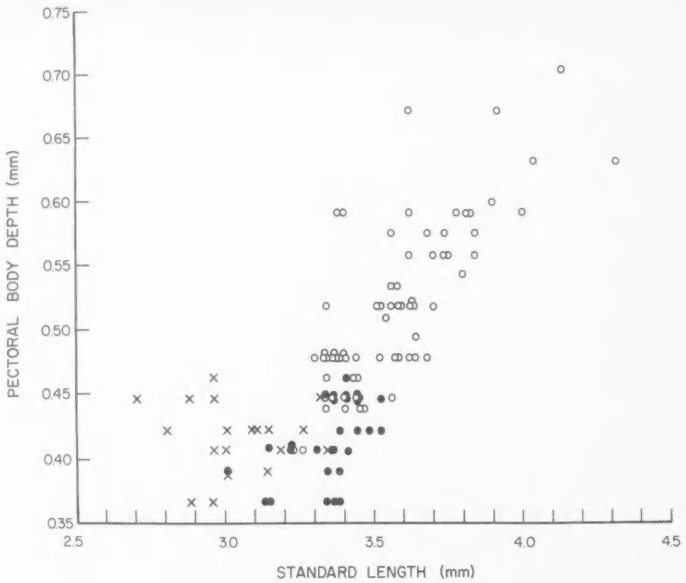


FIGURE 14.—Relationship between pectoral body depth and standard length of *Trachurus symmetricus* larvae which were fed (open circles), starved 1 and 2 days (dots), and starved 3 days (x's).

HL, and 11) bd-2/HL. Standard length was used in ratios and not as a unit to allow discrimination between fed and starved larvae of the same length. To discriminate between the two groups, the analysis selected a set of five variables, listed in the order of selection: 1) bd-2/SL, 2) bd-2/HL, 3) bd-1/HL, 4) ed/SL, and 5) bd-1. With these five variables, 83% of the fed and 86% of the starved larvae in the select size class were correctly classified. When all the larvae, 69 fed and 48 starved (Figure 14), were included in the analysis and the discriminant functions derived from the above five variables were used, 87% of the fed and 94% of the starved were correctly classified.

Comparison of Histological and Morphological Techniques

All larvae classified using morphometric characters were also analysed histologically (Table 1). The histological grading system classified 83% of the larvae which were fed into the healthy group and 83% of the larvae deprived of food for 3 days into the starved group. The histological grades of 1- and 2-day starved larvae were not as well defined; 19% of the cases were graded as healthy, 44% were graded intermediate, and 37% were graded starved. This outcome was similar to results of the initial histological study of 2-day starved larvae reported under Histological Results.

In the morphometric SWDA (Morphological Results), all the starved larvae (1-, 2-, and 3-day starved) were entered into the analysis as one group (n = 48). However, from the above histological grades of the starved larvae, the class should be divided into two groups, early starvation (including 1- and 2-day starved larvae which received all three histological grades) and prolonged starvation (including 3-day starved larvae which were mostly graded as starved). Preliminary laboratory experiments supported this decision. Food was offered to 1-, 2-, and 3-day starved larvae and some 1- and 2-day starved larvae did initiate feeding. No 3-day starved larvae ate food. The

TABLE 1.—Histological classification of *Trachurus symmetricus* larvae.

Item	n	Average histological grade		
		Healthy 2.34-3.00	Intermediate 1.67-2.33	Starved 1.00-1.66
Days fed:				
1	14	12	1	1
2	15	13	2	—
3	15	11	4	—
4	6	6	—	—
5	14	11	3	—
Days starved:				
1	13	3	5	5
2	14	2	7	5
3	18	2	1	15

feeding capability reported for other pelagic fish larvae, after an initial period of starvation, was similar to jack mackerel (Blaxter 1965; Lasker et al. 1970; May 1971). Because of these variables, the morphometric analysis was refined further to differentiate three groups.

Two methods of analyzing the morphometric data for three predetermined groups (fed, early starvation, and prolonged starvation) were examined using 1) all 11 variables previously described, and 2) the set of 5 variables chosen to discriminate between fed and starved larvae morphometrically. In the first test, the SWDA selects the best set of variables to discriminate between the three groups and in the second test, the analysis separates groups with a given set of variables.

The variables selected by the first test (in order of selection) were: 1) bd-2, 2) bd-2/SL, and 3) HL. The set of three variables correctly classified 84% of the fed larvae, 93% of the early starved larvae, and 79% of the prolonged-starved larvae (Test 1, Table 2). The inclusion of two more variables, bd-2/HL and bd-1/HL, did not improve the classification scores. The second test, using the previously chosen set of five variables, correctly classified 84% of the fed larvae, 90% of the early starved, and 74% of the prolonged-starved larvae (Test 2, Table 2). The first test had a better score for both the early and prolonged starvation groups, but either set of variables is a reliable predictor of larval condition.

TABLE 2.—Morphological classification of *Trachurus symmetricus* larvae. The number of larvae in the predicted groups (experimental conditions) is compared with the actual group membership determined by a stepwise discriminant morphometric analysis. Test 1 uses a set of three variables: posterior body depth, posterior body depth divided by standard length, and head length, and Test 2 uses a set of five variables: posterior body depth divided by standard length and head length, pectoral body depth divided by head length, eye diameter divided by standard length, and pectoral body depth.

Experimental conditions	*n*	Fed	Starved	
			1 and 2 days	3 days
		Group membership test 1		
Fed	69	58	10	1
Starved:				
1 and 2 days	29	1	27	1
3 days	19	0	4	15
		Group membership test 2		
Fed	69	58	10	1
Starved:				
1 and 2 days	29	2	26	1
3 days	19	1	4	14

Either the morphological or the histological technique can be used to identify fed larvae and 3-day starved larvae (Table 3). Fifty-three of the 64 (83%) larvae which were offered food were classified as fed (column 2) by the morphometric SWDA and as healthy (column 3a) by the histological method; but, only 44 of these larvae had the score in common (Table 3). Within the 3-day starved group, 14 of the 18 (78%) larvae were correctly classified (column 2) with the morphometric analysis and 15 (83%) were labelled correctly with the histological technique; 13 larvae had the starved score in common. It is difficult to compare the morphological and histological scoring of the early starvation (1- and 2-day starved) group. The morphometric analysis was extremely sensitive for selecting this group, 96% were correctly classified; however, the histological analysis may be more accurate for indicating which larvae in this group can still feed. Five of the 27 (19%) early starved larvae were histologically graded as healthy and may be capable of feeding. It is also possible that intermediate grade larvae (44%) would eat if exposed to food. Eleven of the 12 fish in this intermediate group had a score in common with the morphometric analysis. Intermediate larvae exhibit some tissue degeneration which may be reversible. Additional laboratory experiments are required to determine survi-

TABLE 3.—*Trachurus symmetricus* larvae were fed or starved for 1, 2, or 3 days (column 1). Each larva was classified with the morphometric method (column 2) and the histologic method (column 3). The percent of the larvae correctly classified with each method and the number of larvae correctly classified by both methods is also indicated.

Experimental conditions[1] (1)	Morphometric analysis (2)		Histological analysis (3)		
			Healthy	Intermediate	Starved
		n	53/83%	10	1
Fed *n* = 64	Fed	53/83%	44	8	1
	Starved 1 and 2 days	10	8	2	0
	Starved 3 days	1	1	0	0
		n	5	12/44%	10
Starved 1 and 2 days *n* = 27	Fed	1	0	1	0
	Starved 1 and 2 days	26/96%	5	11	10
	Starved 3 days	0	0	0	0
		n	2	1	15/83%
Starved 3 days *n* = 18	Fed	0	0	0	0
	Starved 1 and 2 days	4	1	1	2
	Starved 3 days	14/78%	1	0	13

[1]The total number of larvae within each experimental group agrees with Table 1 but differs from Table 2 because several larvae were lost during the microtechnique procedure.

val when feeding is only delayed for 1 or 2 days and to ascertain whether tissue degeneration noted during the period of early starvation is reversible.

DISCUSSION AND CONCLUSION

The effects of starvation could be seen throughout the body of larval jack mackerel. There was atrophy of all tissues, with the digestive tract and its associated glands the first tissues affected by starvation. The extent of cellular deterioration increased with time of starvation. Many histological changes, which were associated with starvation in jack mackerel, were similar to changes described in other starving fish larvae: 1) atrophy and cellular and nuclear degeneration of the liver (yellowtail, Umeda and Ochiai 1975; northern anchovy, O'Connell 1976; plaice, Karl Ehrlich pers. commun.), 2) separation of muscle fibers (northern anchovy, O'Connell 1976; herring and plaice, Ehrlich pers. commun.), 3) cellular and nuclear degeneration in the pancreas (yellowtail, Umeda and Ochiai 1975; northern anchovy, O'Connell 1976), and 4) decrease in the size of the epithelial cells in the digestive tract (pike and carp, Kostomarova 1962; yellowtail, Umeda and Ochiai 1975; herring and plaice, Ehrlich et al. 1976; northern anchovy, O'Connell 1976). Some histological changes present in starved jack mackerel larvae, enlargement of the gallbladder and deterioration of the primitive brain cells, have not been reported for other starved fish larvae.

The onset of starvation in jack mackerel larvae was manifested as 1) a change in acinar arrangement of the pancreatic cells and 2) a sloughing of mucosal cells from the midgut into the lumen. These two criteria were shown to be critical variables and were histologically graded to assess the nutritional condition of jack mackerel larvae. O'Connell (1976) reported that the condition of the pancreas was of primary importance for classifying starving northern anchovy larvae. His criteria for good pancreatic condition depended on the abundance of zymogen as well as continuity of cellular structure. The presence of zymogen was not used as a criterion to classify jack mackerel larvae; absence of zymogen was usually associated with feeding, however, the correlation was not consistent. O'Connell also noted mucosal cells in the midgut of larval anchovy but he did not grade this feature. Love (1970) suggested that sloughed midgut cells may be used as an energy source.

During starvation, growth was retarded, larvae shrank, and the soft tissues collapsed causing larvae to look abnormal; the body became bent and thin and the head disproportionately large. An array of larval fish morphometric characteristics have been associated with nutritional condition. A decrease in depth of the larval body has been considered to be an important indicator of starvation although Blaxter (1971) did not find it to be a sensitive character for elongate clupeoid larvae. However, body depth divided by standard length appears to reflect the condition of postlarval anchovy (Nakai et al. 1969) and older, larval northern anchovy (Arthur 1976), but the ratio did not identify feeding and starving post yolk-sac northern anchovy (O'Connell 1976). Nakai et al. (1969) also related the diameter of the posterior digestive tract to condition in postlarval anchovy. The height of the body in the posterior part of the trunk was measured by Honjo et al. (1959) and was found to differ between postlarval anchovy collected from two fishing grounds. Honjo et al. (1959) suggested that the anatomical difference was indicative of a higher availability of food organisms in one area than in the other. Another predictive parameter for the condition of post yolk-sac larvae was the relative condition factor reported by Ehrlich et al. (1976) for herring and plaice. Its estimation involves weighing each larva. All of the above mentioned morphological criteria reflect larval nutritional condition and may be considered reference parameters, but no one criterion accurately identifies larval condition on an individual basis. The lack of sensitivity of a single morphometric indicator may be due to natural variability alone or more probably to the rapid morphological changes which occur in larval fish. For example, Zweifel[3] using the data of Hunter (1976b) has shown that for feeding northern anchovy larvae the condition factor weight/length^3 was neither constant nor monotonic even when food densities were carefully controlled. For variation in food levels (including no food) it would be expected that there should be even more complex relationships.

Even though the histological and morphological techniques have proven to be effective for predicting condition of laboratory-reared animals, both techniques must be field tested with wild-caught

[3]Zweifel, J. 1977. A non-linear model for allometry in larval fish. Unpubl. manuscr., 25 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

larvae. Evidence of morphological differences between laboratory-reared and sea-caught larvae indicates that it may be difficult to transfer laboratory results to the sea. Blaxter (1968, 1971), for example, found laboratory-reared herring larvae exhibited a greater size variation and a higher condition factor than sea-caught larvae. Balbontin et al. (1973) reported differences in body depth, head depth, and head length between laboratory and wild herring juveniles of the same length. The laboratory-reared animals had a deeper body and a deeper or longer head.

The usefulness of the morphometric discriminant technique will depend upon the consistency of changes in morphological pattern in individuals when feeding and starving. However, even if the changes are not constant, useful indicators of larval survival will not require the exact allocation of all individuals into feeding and starving groups but rather only reasonable estimates of the relative proportions will be needed. My results indicate that a multivariate statistical approach, combining several morphometric measurements in a SWDA, may provide this information. Species that do not yield to a morphological analysis should yield to the histological approach.

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IDENTIFICATION OF STOCKS OF BRISTOL BAY SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, BY EVALUATING SCALE PATTERNS WITH A POLYNOMIAL DISCRIMINANT METHOD[1]

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ABSTRACT

A polynomial discriminant method is developed for the racial classification of stocks of sockeye salmon. The method is based upon the nonparametric estimation of the multivariate probability densities of the scale characteristics for each stock considered. Errors in classification are examined and a correction procedure is extended to the n-class case. As an example, sockeye salmon of age 2.2 sampled on the high seas are classified to river of origin based on freshwater scale growth patterns. Also, freshwater and marine scale characters are evaluated for stock identification purposes involving certain Bristol Bay runs.

Racial analysis of high-seas salmon has important applications both in life history studies of various stocks and in management considerations of these stocks. As a result, many have examined the characteristics of scale structure to differentiate salmon subpopulations. Konovalov (1971) notes that some investigators were ignoring many characteristics in scale structure which arise under the effects of ecological factors in specific bodies of water. When the ecological conditions affecting scale characters are seriously considered, statistically significant differences between subpopulations can often be found. The ability to recognize salmon subpopulations depends upon the differences between the stocks in terms of examined characteristics and the accuracy of the analytic technique. Various discriminant function analyses have been traditionally used.

Fukuhara et al. (1962), Amos et al. (1963), and Dark and Landrum (1964) used linear discriminant functions based upon morphological characteristics to identify the continent of origin of Pacific salmon. Scale characteristics and linear discriminant functions were used by Anas (1964) and Mason (1966). Anas and Murai (1969) used linear and quadratic discriminant functions. Recent investigations by Major et al. (1975) and Bilton and Messinger (1975) used unspecified discriminant function techniques, probably similar to those of Anas and Murai (1969). These and other studies show the utility of discriminant function methodology for identifying races of Pacific salmon.

Salmon managers need a flexible and easily implemented stock identification technique. This paper applies a generalized discriminant function technique to measurements of sockeye salmon scales to attempt to fulfill this need.

DISCRIMINANT FUNCTION ANALYSES OR PATTERN RECOGNITION[4]

Discriminant function analysis depends on the recognition of underlying patterns differing among classes of objects. In this case, scale patterns characterize a sockeye salmon of a particular origin. A set of p-scale characters (a p-tuple or vector in p-space) measured on an individual salmon provides a description of that salmon. A sample of p-tuples for a number of salmon from one origin (the learning sample) establishes a region in p-space characteristic of that class of sockeye. Samples from salmon of different and known origins establish regions in p-space which may be separated by decision surfaces. A sockeye salmon of unknown origin may be classified according to which region its p-tuple occupies. The accuracy of classification depends upon the precision with

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[4]A good text on pattern recognition is given by Patrick (1972). A review of the literature is given by Das Gupta (1973).

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which the regions are described and the inherent separation between them.

These regions are described mathematically by multivariate probability density functions. Fisher's (1936) linear discriminant function defines a linear decision surface (hyperplane) derived by describing these regions as multivariate normal density distributions with common variance-covariance matrices (Welch 1939). Quadratic discriminant functions have been developed (Smith 1947). The resulting decision surfaces are nonlinear. The quadratic discriminant function does not require common variance-covariance matrices. Anas and Murai (1969) compared the classificatory abilities of the linear and quadratic discriminant functions. They found (in agreement with Isaacson 1954) that even if the assumption that the distributions have common variance-covariance matrices is violated, the linear discriminant function would still give good results for large sample sizes. But the quadratic function gave slightly better results.

All investigators utilizing discriminant analyses to separate races of Pacific salmon have assumed that the density distributions of measurements from a particular class of salmon were multivariate normal. The frequency distributions of scale characters in Major et al. (1975) show that multimodal and skewed distributions occur for chinook salmon scale characters even in the univariate case. In many other cases, the underlying distribution functions may be non-Gaussian. Discriminant functions based upon non-Gaussian distributions or obtained by distribution-free methods are preferable to those based upon an unrealized assumption of normality.

Nearly all of the discriminant function analyses used in the investigations of Pacific salmon have been two-class analyses designed to determine the continent of origin of salmon taken on the high seas. For the two-class situation only one discriminant function need be calculated. These two-class problems are a special case of the many-class problems in which a separate discriminant function is calculated for each class. Bilton and Messinger (1975) calculated discriminant functions for each of several runs in a classification study on sockeye salmon. If several stocks of salmon intermingle and are to be classified, analyses of this type are needed.

Specht's (1966) polynomial discriminant method does not require that the underlying density distributions be multivariate normal nor that they have common variance-covariance matrices. Since this method is nonparametric, various scale characteristics may be used for discrimination with no particular regard to the underlying distributions. Thus, the method is flexible and practical.

Specht (1966) uses an estimated probability density function of the form described by Parzen (1962) and extended by Murthy (1966) to the multivariate case. The underlying multivariate density for each class is modeled by a sum of functions that are multivariate Gaussian in form, one such function for each fish in the learning sample for that class. This set of functions is complete. Therefore, for each class the underlying continuous probability density, Gaussian or not, may be approximated arbitrarily closely by such a sum. A power series expansion of this estimated denisty then results in a polynomial term in the density function, the coefficients of which are functions of the observations (fish) in the learning sample. One such set of coefficients is computed for each class to be considered. These polynomials determine the nonlinear decision surfaces and are the basis for discrimination.

The individual multivariate Gaussian functions (which when summed model the underlying multivariate distribution for that class) contain a "smoothing parameter," σ, which appears in the place of a standard error. This parameter is then incorporated in the estimates of the polynomial coefficients. The reader is referred to Specht (1966) for a discussion of the effect of this smoothing parameter and for the algorithm for the calculation of the sets of polynomial coefficients $\{D_{k_i \ldots k_j \ldots k_h}\}$. The polynomial discriminant function is:

$$
\begin{aligned}
P(X) = {} & D_0 + D_1X_1 + D_2X_2 + \ldots + D_pX_p \\
& + D_{11}X_1^2 + \ldots + D_{k_1k_2}X_{k_1}X_{k_2} \\
& + \ldots + D_{pp}X^2_p + D_{111}X_1^3 \\
& + \ldots + D_{k_1k_2k_3}X_{k_1}X_{k_2}X_{k_3} + \ldots \\
& + D_{ppp}X^3_p + \ldots \\
& + D_{k_1 \ldots k_j \ldots k_h}X_{k_1} \ldots X_{k_h} \\
& + \ldots,
\end{aligned}
$$

where p = dimension of the vector X (set of scale characters)

$1 \leq h_j \leq p$
$j = 1, 2, \ldots, h$
h = the degree of the variable portion of the term.

The decision on an unknown X (set of scale measurements from a salmon of unknown origin) is thus:

$$\text{Choose } d(X) = \theta_r \text{ so that } h_r P^r(X) \geq h_s P^s(X) \text{ for all } s \neq r$$

where $d(X)$ = the decision on an unknown X
θ_i's = the classes (origins)
$p^i(X)$ = the polynomial value for X calculated using the discriminant function for class θ_i
h_i = the a priori probability, the uses of which will be described later.

APPLICATION OF THE METHOD

Three scale sample sets are required to implement the polynomial discriminant method: learning samples, test samples, and unknown samples. The learning and testing samples are collected from each subpopulation when they are segregated (i.e., in the rivers of origin). Scale characters to be measured in the unknown sample for the required discrimination are determined by evaluating characters measured in the learning samples. The learning samples and the characters selected are used to calculate the coefficients in the polynomial discriminant functions. To calculate these coefficients, the value for the smoothing parameter and the point at which the discriminant function should be truncated must be determined. Various circumstances will dictate different choices. When a smoothing parameter of 1.5 was chosen, all terms in the discriminant function greater than the fourth order contributed negligibly to polynomial values and so were truncated in our applications. Often, polynomial discriminant functions of lower order yield adequate results.[5]

[5]A polynomial discriminant function with six variables and of the fourth order will contain 210 terms. Since our calculations were performed by computer, we chose not to delete the third or fourth degree terms. However, if more than six variables are used, it would be wise to truncate further in order to keep the number of terms down.

The fish comprising the test samples are classified to test the effectiveness of the polynomial discriminant method and to determine the a priori probabilities. (Each test sample consists of fish from one class.) Finally, fish collected from the zone of intermingling are classified to determine the degree of intermingling in the area of interest.

Appraisal of the method using scale samples of sockeye salmon collected from the 1967 escapement in five Bristol Bay rivers showed large percentages of fish comprising the test samples were correctly classified. However, misclassified fish in the test group (set of test samples from all rivers being considered) were not assigned to the rivers in proportion to the known relative test sample sizes. To balance these misclassifications, wherever a greater number of fish comprising the test group was assigned to a particular river than should have been (according to the relative test sample sizes), the a priori probability for that river was lowered. Corresponding increases were made for those classes with insufficient assignment. By alternatively using the decision procedure of the polynomial discriminant method and adjusting the a priori probabilities, we obtained solutions so that the number of fish belonging to a certain river that were misassigned to all other rivers approximately equaled the number of fish misassigned to that certain river from all other rivers. Thus the a priori probabilities were not used in the manner their name suggests, but a priori knowledge may dictate test sample sizes. The relative test sample sizes in the test group may be in the relative proportions to be expected in the unknown sample (i.e., historical relative run sizes). The adjustment procedure, then, shifts the nonlinear decision surfaces between the probability densities so that the incorrectly identified samples are assigned to the various rivers in the proportions dictated by the test sample sizes in the test group. However, the primary purpose of the adjustment procedure is not to balance the misclassifications but to maximize the number of correct classifications. As the misclassifications are balanced, the number of correct classifications generally increases. At this point the result is a classification method that maximizes the total number of correct classifications and balances misclassification rates for a test group in which the test sample sizes are in particular proportions.

However, it is obvious that the proportions of fish from the various classes in the test group would rarely be identical to those proportions in

the unknown sample. Thus, imbalance among the misclassified fish will recur, unless the expected accuracy of classification is very good (near 100%). We have devised a method to correct for this.

Based upon the results of classification of the known test group, the classification matrix, C, is estimated:

$$\hat{C} = \begin{bmatrix} \hat{c}_{11} & \hat{c}_{12} & \cdots & \hat{c}_{1n} \\ \hat{c}_{21} & \hat{c}_{22} & \cdots & \hat{c}_{2n} \\ \vdots & \vdots & & \vdots \\ \hat{c}_{n1} & \hat{c}_{n2} & \cdots & \hat{c}_{nn} \end{bmatrix},$$

where $\hat{c}_{ij}$ is an estimate of the fraction of fish allocated to class i belonging to class j, such that $\sum_{i=1}^{n} \hat{c}_{ij} = 1.0, \ \forall j$. (Note that for each j the $\hat{c}_{ij}$'s are a set of estimated multinomial probabilities and that each test sample size should be adequate.) If the discrimination is error-free, C would be an identity matrix. The adjustment of a priori probabilities causes the initially estimated classification matrix to evolve to the point where

$$\hat{C}T = R_t \text{ such that } T \approx R_t.$$

The ith component of the vector T is the fraction of fish in the test group from test sample i (class i), and the ith component of the vector R_t is the fraction of fish in the test group allocated to class i by the adjusted polynomial discriminant method.

The test samples comprising T are not independent of the classification scheme since they are used to determine the a priori probabilities used in the decision rule. Hence, the estimated probabilities in the classification matrix may not be unbiased. However, we did chi-square tests that show elements of the classification matrix are not significantly different when estimated with either the test samples used to determine the a priori probabilities or a second independent test group. Thus, we prefer to use only one test group to determine the a priori probabilities and to estimate the elements of the classification matrix because the test sample sizes will be larger (and the variance of the $\hat{c}_{ij}$'s smaller) if we do not subdivide the fish available.

Now, let u_i be the fraction of fish in a sampled group that belong to the ith class. The vector U is then unknown except for the obvious side condition $\sum_{i=1}^{n} u_i = 1$. The classification matrix now operates on U to give:

$$CU = R_u{}^{6}$$

where the ith component of R_u is the fraction of fish in the unknown sample allocated to the ith class. Since C is estimated, R_u is known and since C is usually nonsingular, we can estimate U by

$$\hat{U} = \hat{C}^{-1} R_u.$$

Each point estimate ($\hat{u}_i$) obtained will have some variance. This variability will depend upon the accuracy with which fish from class i are classified, the accuracy with which the elements of C are estimated, and variance due to sampling error encountered when obtaining the unknown sample. Thus, if any u_i is small, then its estimate ($\hat{u}_i$) may be negative. Such solutions are meaningless. In such cases the classes with negative solutions should be dropped (assume such $u_i \approx 0$) and the analyses repeated.

We did simulation work to evaluate the classification matrix correction procedure for the two- and three-class situations. Five hundred simulated experiments were done for each situation. For the two-class case the average error of the classification results was 0.100 while that of the corrected estimates was 0.055. In 84% of the experiments the corrected estimate was closer to the true value than classification result. For the three-class case the average error of the classification results was 0.127 while that of the corrected estimates was 0.054. In 89% of the experiments the corrected estimate was closest to the true value. The results of these simulations show that the classification correction procedure improves estimates of the true proportion of a class present.

This classification matrix correction procedure will reduce to the correction procedure developed for the two-class case by Worlund[7] in the following manner:

[6] A similar relationship and a least squares solution technique is given by Worlund and Fredin (1962).

[7] Worlund, D. D. 1960. A method for computing the variance of an estimate of the rate of intermingling of two salmon populations. Unpubl. manuscr., 13 p. Bur. Commer. Fish., Biol. Lab., Seattle, Wash.

$$U = C^{-1} R_u$$

or

$$\begin{bmatrix} u_1 \\ u_2 \end{bmatrix} = \begin{bmatrix} \dfrac{c_{22}r_1 - c_{12}r_2}{c_{11}c_{22} - c_{21}c_{12}} \\ \dfrac{c_{11}r_2 - c_{21}r_1}{c_{11}c_{22} - c_{21}c_{12}} \end{bmatrix}$$

Generally $$u_i = \frac{r_i c_{jj} - c_{ij} r_j}{c_{ii}c_{jj} - c_{ji}c_{ij}}.$$

Since $$r_j = 1 - r_i,$$
$$c_{ji} = 1 - c_{ii},$$
$$c_{jj} = 1 - c_{ij},$$

substitution yields $$u_i = \frac{r_i - c_{ij}}{c_{ii} - c_{ij}},$$

which is the correction formula of Worlund and Fredin (1962) (except for differences in notation and terminology) that has been used in many two-class Pacific salmon stock identification studies.

Application to Sockeye Salmon Samples Taken in High Seas Sampling

A problem of interest to the nations bordering the North Pacific Ocean is the origin of sockeye salmon taken on the high seas. The rivers of origin of sockeye salmon south of the central Aleutian Islands in summer are of particular interest to the United States since an index of their overall relative abundance is used to forecast the numbers of mature fish returning to Bristol Bay in the following year (Rogers 1975). These fish are primarily of Bristol Bay origin (Hartt 1962, 1966; Hartt et al. 1975). Knowledge of the relative abundance of the various runs of the Bristol Bay stock south of the central Aleutians would be useful for forecast purposes and might provide insight into the high seas life history of the various runs.

In order to recognize age 2.2 immature sockeye salmon on the high seas in 1976, the freshwater growth patterns of scales from three of the major rivers in Bristol Bay were examined.[8] Scales from the smolt outmigrations of 1974 for the Kvichak and Naknek Rivers were used as learning and testing samples. For the Egegik River scales from age 2.2 adult fish returning to spawn in 1976 were used as learning and testing samples because smolt scales were unavailable. The freshwater scale patterns of fish from these runs were used to classify the sockeye salmon captured south of Adak Island during summer 1976 after having spent two winters in the ocean.

The scale patterns were examined under a microprojector of the type described by Dahlberg and Phinney (1968). The widths of the summer, winter, and plus growth zones were measured in terms of circuli counts and distance. The width of the widest circulus was also measured. Each scale character was then ranked over all classes (rivers) and the Kruskal-Wallis statistic (Kruskal and Wallis 1952) calculated. The difference between the average sum of ranks for each pairwise class combination was also calculated. On the basis of these statistics the scale characters providing the best univariate separation were selected for use in the polynomial discriminant method. Highly dependent scale characters were not used.

By examining the learning samples, six scale characteristics were chosen for use in the polynomial discriminant method: 1) The number of the circuli in the first winter growth zone, 2) the number of circuli in the second summer growth zone, 3) the number of circuli in the plus growth zone, 4) the width of the first summer growth zone, 5) the width of the second winter growth zone, and 6) the width of the widest circulus.[9] Learning sample sizes of 25, 25, and 24 for the Egegik, Kvichak, and Naknek River classes, respectively, were used to calculate the coefficients in the polynomial function for each class. The classificatory ability of these functions was then tested.

The relative test sample sizes for each class were determined by examining run size data. According to the average run sizes of age 2.3 salmon for the last 8 yr approximately equal numbers of fish from each class were expected to occur in the unknown sample. However, since the Kvichak River test sample size was twice that of the Egegik or Naknek River sample size, the fish in the latter test samples were given a weight of 2 when the a priori

[8]Age designation indicates fish which migrated to sea after two winters in freshwater and have spent two winters at sea. They are expected to return from the ocean primarily at age 2.3, or after spending three winters at sea.

[9]It should be mentioned that all data points were "normalized." That is, the mean and standard deviation for each scale character were calculated from the learning samples (all categories combined). All data points were then transformed by subtracting off the mean and dividing by the standard deviation for the appropriate scale character. This is done for numerical purposes.

probabilities were adjusted. After adjusting the a priori probabilities, we obtained the results given in Table 1. The classification matrix was then estimated:

$$\hat{C} = \begin{bmatrix} 0.800 & 0.040 & 0.167 \\ 0.080 & 0.740 & 0.208 \\ 0.120 & 0.220 & 0.625 \end{bmatrix}$$

where the subscripts of the matrix elements ($\hat{c}_{ij}$'s) were 1, 2, and 3 for the Egegik, Kvichak, and Naknek River classes, respectively. Seventy-two percent of the fish in the test group were correctly classified. The fish in the high seas sample were then classified with the adjusted polynomial discriminant method.

Of the 101 sockeye salmon, 25 were classified as Egegik River fish, 22 as Kvichak River fish, and 54 as Naknek River fish. The resultant vector was:

$$R_u = \begin{bmatrix} 0.267 \\ 0.222 \\ 0.511 \end{bmatrix}.$$

The estimated unknown vector was thus:

$$\hat{C}^{-1} R_u = \begin{bmatrix} 1.300 & 0.037 & -0.360 \\ -0.078 & 1.498 & -0.478 \\ -0.222 & -0.534 & 1.837 \end{bmatrix} \begin{bmatrix} 0.267 \\ 0.222 \\ 0.511 \end{bmatrix}$$

$$= \begin{bmatrix} 0.171 \\ 0.067 \\ 0.761 \end{bmatrix} = \hat{U}.$$

Based upon preliminary data for the 1977 Bristol Bay sockeye salmon run from the Alaska Department of Fish and Game, the actual unknown vector was:

$$U = \begin{bmatrix} 0.325 \\ 0.061 \\ 0.614 \end{bmatrix}.$$

The classification matrix correction procedure gave a slightly better estimate than the direct results of the polynomial discriminant method. The differences between the u_i's and the $\hat{u}_i$'s were due to bias and variability. (We are presently examining methods to reduce the variability of our $\hat{u}_i$'s.)

A problem with the high seas sample is that some of these sockeye salmon originate in rivers other than those considered. Although the three classes considered will account for nearly all of the age 2.2 sockeye salmon bound for Bristol Bay, some may be non-Bristol Bay fish. When the Bristol Bay runs are at a low point in their cycle, up to 20% of the high seas sockeye salmon at Adak Island may be non-Bristol Bay fish (Hartt et al. 1975). The possible bias from classifying the non-Bristol Bay fish into the classes established should be considered since 1977 is a low year in the sockeye salmon run cycle.

TABLE 1.—Results of the polynomial discriminant method on a known test group of Bristol Bay sockeye salmon. The a priori probabilities were 0.340, 0.332, and 0.328 for the Egegik, Kvichak, and Naknek River classes, respectively.

Calculated decisions	Correct decisions			Total (all calculated decisions)
	Egegik	Kvichak	Naknek	
Egegik	40	2	8	50
Kvichak	4	37	10	51
Naknek	6	11	30	47
Total (all correct decisions)	50	50	48	148

In conclusion, the polynomial discriminant method can be used to identify certain runs of sockeye salmon on the high seas by differences in freshwater scale growth patterns. Possibly the relative proportions of sockeye salmon that will be returning to inshore areas can be predicted. Eventually the method will be used to predict one year in advance the relative run sizes to the major Bristol Bay rivers by sampling these sockeye on the high seas.

Application to Inshore Fishery Stock Separation

A problem of interest to the Alaska Department of Fish and Game is the separation of stocks in commercial catches in inshore areas, particularly the separation of Kvichak, Naknek, and Egegik River sockeye salmon. The Division of Commercial Fisheries is collecting data on scale measurements for growth studies. They are interested in how well these data and the polynomial discriminant method can separate Bristol Bay sockeye salmon stocks.

Scale data from samples of the 1973 spawning escapement were examined. Each of two age-classes was examined separately. Distance and circuli counts to both the freshwater and saltwater annuli were examined for use in the polynomial discriminant method with the Kruskal-Wallis and multiple comparison procedures. The accuracy of classification for age 1.2 and age 2.2 sockeye salm-

on was examined for each age-group with known test groups.

The degree of separation for age 1.2 sockeye salmon is shown in Table 2. (Egegik River fish are historically insignificant in this age-class.) The scale characters providing this separation were: 1) the circuli count to the first annulus, 2) the distance to the first annulus, 3) the distance from the first to the second annulus, 4) the distance from the second to the third annulus, 5) the circuli count from the third annulus to the edge of the scale, and 6) the distance from the third annulus to the edge of the scale. Ninety-five percent of the fish in the test group were correctly classified.

The degree of separation for age 2.2 sockeye salmon is shown in Table 3. The scale characters providing this separation were: 1) the circuli count to the first annulus, 2) the distance to the first annulus, 3) the circuli count from the first to the second annulus, 4) the distance from the second to the third annulus, 5) the distance from the third to the fourth annulus, and 6) the circuli count from the fourth annulus to the edge of the scale. Seventy-seven percent of the fish in the test group were correctly classified.

Thus, the polynomial discriminant method can provide adequate separation with a given data base. The data collected for growth studies provide good separation in some cases. Sockeye salmon from the Egegik, Kvichak, and Naknek Rivers are distinguishable in terms of these scale measurements and it should be possible to estimate their relative proportions in catch samples.

TABLE 2.—Results of the polynomial discriminant method on 1.2 age Bristol Bay sockeye salmon from 1973. The a priori probabilities were 0.52 and 0.48 for the Kvichak and Naknek River classes, respectively.

Calculated decisions	Correct decisions		Total (all calculated decisions)
	Kvichak	Naknek	
Kvichak	18	0	18
Naknek	2	19	21
Total (all correct decisions)	20	19	39

TABLE 3.—Results of the polynomial discriminant method on 2.2 age Bristol Bay sockeye salmon from 1973. The a priori probabilities were 0.342, 0.330, and 0.328 for the Egegik, Kvichak, and Naknek River classes, respectively.

Calculated decisions	Correct decisions			Total (all calculated decisions)
	Egegik	Kvichak	Naknek	
Egegik	20	3	3	26
Kvichak	1	22	4	27
Naknek	5	1	14	20
Total (all correct decisions)	26	26	21	73

COMMENTS AND CONCLUSIONS

The key to successful implementation of the polynomial discriminant method is the choice of scale characters that reflect differences between the subpopulations of concern. The scale characters that are most likely different are those that are formed when the populations are geographically separated. Genetic and environmental influences on scale formation probably interact to create these differences. Although it is likely that no single characteristic will provide the required separation, a group of characteristics analyzed with multivariate techniques (e.g., the polynomial discriminant method) will often provide this required separation. The polynomial discriminant function technique requires no consideration of the underlying probability density functions for these scale characters because these density functions are estimated nonparametrically. Once the characters that provide the best separation are determined (by rank order comparison procedures in this paper) the discriminant function analysis may be implemented.

A learning sample is needed to calculate the discriminant function for each subpopulation. These fish comprising these samples must be collected before or after the populations intermingle (either as smolts or returning adults in the respective rivers). Learning samples must be taken from the same year class and freshwater age-group as the unknown (mixed) population if the scale characters are known or thought to vary from year to year. Using Specht's (1966) algorithm and the data from these learning samples, the coefficients in the discriminant functions are calculated. The next step is to appraise the effectiveness of these polynomial discriminant functions.

By classifying a group of test samples the proportion of correctly identified fish and the classification error rates can be determined. The proportion of correctly identified fish will likely be low until a good set of a priori probabilities is determined. As the a priori probabilities are adjusted to balance the classification error rates, the proportion of correctly identified fish will generally increase. The proportion of correctly identified fish, when the classification error rates are satisfactorily balanced, gives an indicator of the effectiveness of the polynomial discriminant method. The classification error rates specific to these final a priori probabilities are now estimated so that they may be corrected for when the polynomial discriminant

method is applied to the unknown mixed sample. This is done with the classification matrix correction procedure.

First, the fish in the unknown mixed sample are classified with the polynomial discriminant method (using the adjusted a priori probabilities). The proportions resulting for each subpopulation and the decision matrix allow simple algebraic solution for the estimated true proportions of the various subpopulations in the zones of intermingling.

Estimates of this type are often needed in particular management situations involving Pacific salmon. By using scale samples and the polynomial discriminant method, the proportions of the major classes present in areas where the subpopulations mix can be estimated. We have considered only two possible applications in this paper: high seas monitoring for predictive purposes and the analysis of catch samples. Many other possibilities exist for other situations and other salmon species: the timing of inshore runs could be examined in estuarine areas or in river systems, the continent of origin of salmon on the high seas could be examined (for those species or areas not already analyzed), or the intermingling of hatchery and native populations could be analyzed for certain fisheries. Since scale samples are relatively easy to collect and exchange and since computers are readily available to do the necessary calculations, the polynomial discriminant method is a flexible and practical tool for the racial analysis of Pacific salmon, particularly sockeye salmon.

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EFFECTIVENESS OF ESCAPE VENT SHAPE IN TRAPS FOR CATCHING LEGAL-SIZED LOBSTER, *HOMARUS AMERICANUS*, AND HARVESTABLE-SIZED CRABS, *CANCER BOREALIS* AND *CANCER IRRORATUS*[1]

JAY S. KROUSE[2]

ABSTRACT

During 1976 a study was conducted to find an escape vent that would select similar sized lobsters as the rectangular vent, yet retain *Cancer* crabs ≥90 mm carapace width. Analysis of the size composition of research and commercial catches from experimental traps revealed that circular (58 mm in diameter) and rectangular (44.5 × 152.4 mm) vents release shorts and retain legal lobsters (≥81 mm carapace length) equally well, and decidedly more marketable-sized crabs were captured in traps with circular vents. Length-width relationship shows that crabs ≥90 mm carapace width have lengths ≥58 mm, thus precluding the possibility of marketable-sized crabs exiting through an opening 58 mm in diameter. Escapement studies for lobsters confirm that with the present minimum legal size of $3^{3}/_{16}$ in, a 58-mm diameter vent will select legals and allow most of the sublegals to escape.

Accordingly, the Maine Department of Marine Resources recommends that either circular (≥58 mm in diameter) or oblong (≥44.5 × 152.4 mm) escape vents be incorporated in all crab and lobster traps along the Maine coast.

Although rectangular escape vents are a very beneficial type of savings gear for the lobster fishery (Templeman 1939; Wilder 1945, 1948, 1954; Krouse and Thomas 1975; Krouse 1976), this vent does not retain marketable-sized rock crab, *Cancer irroratus*, and Jonah crab, *C. borealis*. Since these commercially important crab species are often caught incidental to lobsters, I undertook the present study to find an escape opening that would retain harvestable-sized crabs and have similar fishing selectivities for the lobster, *Homarus americanus*, as the rectangular vent.

In designing a trap to catch crabs and exclude lobsters, Stasko (1975) observed in laboratory tests that circular holes retained commercial-sized crabs yet allowed small lobsters to escape; however, the effectiveness of escape holes was not tested in the field. Jow (1961) demonstrated the advantages of circular escape openings in the trap fishery for Dungeness crab, *C. magister*.

In this paper I evaluate the relative efficiency of circular and rectangular vents by examining data from: 1) commercial and research catches compiled from vented and nonvented traps; 2) studies of escapement from traps; and 3) certain morphometric relationships of crabs and lobsters.

METHODS

From November 1976 through March 1977 a commercial fisherman recorded and provided me with catch data from traps with circular vents (58-mm diameter) fished alongside traps without vents. This experimental gear was arranged into two groups with four trawls [series of six traps spaced about 6 fathoms (11.0 m) apart with a surface buoy at either end] per group. In each group half the traps in a trawl had no vents, while the remainder had either single (end of trap) or paired (side of trap) vents depending upon the group (Figure 1B, D). Every time the fisherman hauled these traps he recorded the following information: 1) number of days traps were set between hauls; and 2) number of lobsters ≥81 mm carapace length, CL (keepers), and <81 mm CL (shorts) caught in the vented and nonvented traps for each trawl string.

From July through November 1976, project personnel fished commercial lobster traps near

[1]This study was conducted in cooperation with the U.S. Department of Commerce, National Marine Fisheries Service, under Public Law 88-309, as amended, Commercial Fisheries Research and Development Act, Project 3-153-R.

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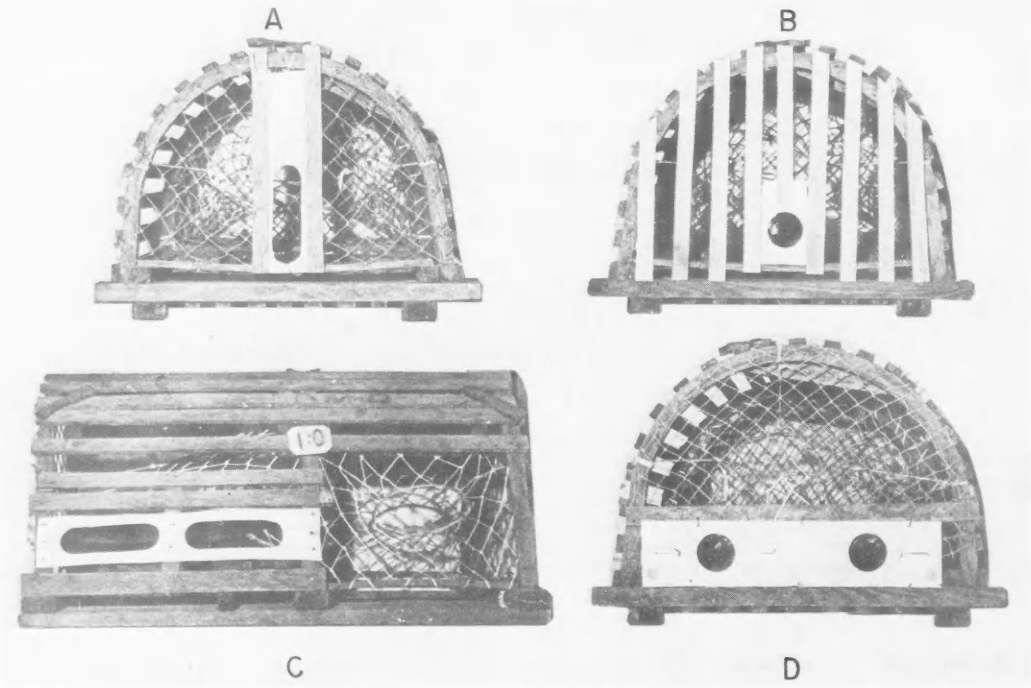

FIGURE 1.—Lobster traps having a rectangular vent positioned vertically (A) and horizontally (C) and single (B) and paired (D) circular vents.

Boothbay Harbor, Maine, with: 1) circular [58-mm (2.3 in) and 61-mm (2.4 in) diameter] vents; 2) vertical and horizontal rectangular [44.5 mm (1.8 in) × 152.4 mm (6.0 in)] vents; and 3) traps without vents. Carapace length of lobsters was measured from posterodorsal edge of eye socket to posterior margin of carapace and carapace width (CW) of crabs, distance between the two most posterior notches on the anterolateral border of the carapace, to the nearest millimeter.

Trap escapement was studied by placing lobsters of known sizes in traps with circular openings of 58, 60, and 61 mm in diameter. Side entrances of each trap were closed so escapement had to be via the vents. Traps were secured to the laboratory dock and usually checked daily for escapement for about a week.

To determine whether or not a crab or lobster could pass through a round opening of a given size, we correlated carapace length of lobsters with carapace height (CH), and the carapace width of crabs with carapace length. For 217 lobsters (sexes combined), ranging from 70 to 98 mm CL, carapace height was determined by positioning the lobster's ventral surface on a flat board and then measuring the greatest perpendicular distance from the board to the top of the carapace. Carapace length of crabs was measured from the anterior margin of the frontal region to the posterior border of the intestinal region. Measurements for the two *Cancer* species were treated separately due to the species disparities in body shapes. We recorded carapace length for 103 male rock crabs (females were excluded due to commercial unimportance) ranging from 90 to 122 mm CW, and 96 Jonah crabs (sexes combined) ranging from 96 to 132 mm CW.

RESULTS AND DISCUSSION

Lobsters in Research Gear

There are marked differences in size composition and number of lobsters caught in nonvented

TABLE 1.—Lobsters caught with nonvented and various types of vented traps from July through November 1976.

	Catch				Catch effort		
Vent type	Total no.	Sublegals: legals	Mean carapace length (mm)	Standard error	Legals per trap haul	No. of trap hauls	Months fished
Nonvented	749	4.3:1	76.2	±0.28	0.53	265	July-Nov.
Horizontal	198	0.6:1	83.9	±0.62	0.54	229	July-Nov.
Vertical	107	0.5:1	84.3	±1.05	0.56	129	July-Sept.
Circular:							
58 mm	25	0.6:1	82.8	±1.35	0.30	53	Oct.-Nov.
61 mm	42	0.4:1	85.9	±1.35	0.47	66	Sept.

and vented traps (Table 1). Vented traps caught fewer sublegal lobsters per trap-haul than nonvented traps (t-test, $P<0.01$).

The ratio of sublegal to legal lobsters did not differ among the four types of vents (t-test, $P>0.1$), with the exception of 61-mm circular vents which caught fewer sublegals than horizontal vents ($P<0.01$). As will be discussed later, the 61-mm hole is slightly oversize for a minimum size of 81 mm CL, thus some smaller legal lobsters and most shorts escape. Nevertheless this information suggests that circular openings are as effective as the rectangular vent (Krouse and Thomas 1975) in permitting escapement of short lobsters.

To further assess the relative efficiencies of the various vents, catch-effort values (numbers of lobsters per trap haul set over day, CPUE) were calculated and plotted for legal-sized and all-sized lobsters combined for each vent type (Figure 2). For this figure, 58- and 61-mm circular vent data were pooled because of the small sample size and similar catch values. Figure 2 graphically shows that the CPUE for legal-sized lobsters was similar for all vent types; however, for combined catches of legals and sublegals, the CPUE for nonvented traps was several fold greater. Thus, this indicates that all traps tested were about equally efficient in capturing legal lobsters; but, as to be expected, nonvented traps caught substantial numbers of short lobsters which probably would have escaped from vented traps. Most importantly, these data support an earlier conclusion that circular vents select about the same size lobsters as do rectangular vents.

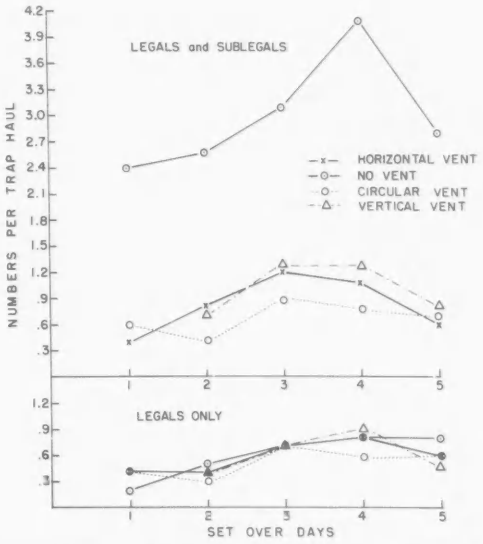

FIGURE 2.—Comparison of the number of lobsters (legals only; sublegal and legals combined) per trap haul set over day for lobster traps with rectangular (horizontal and vertical) and circular vents (58 and 61 mm combined) and traps without vents.

Lobsters in Commercial Gear

Catch data provided by a local lobsterman were compiled according to the following categories of gear: 1) end vented traps with a single circular hole of 58 mm diameter (Figure 1B); 2) side vented traps with paired round openings of 58 mm diameter (Figure 1D); and 3) two groups of nonvented traps (one for nonvented traps fished in the same trawl string with end vented traps and the second for traps paired with side vented traps). Comparisons of the CPUE and the ratios of sublegals to legals indicated that vented traps caught fewer sublegal-sized lobsters than the corresponding groups of nonvented traps (t-test, $P<0.01$) (Table 2). Higher CPUE values for vented traps show that circular vents are at least as efficient if not more effective in catching legal-sized lobsters than nonvented traps (t-test, $P<0.01$). In an earlier study Krouse and Thomas (1975) reported that traps with 44.5 × 152.4 mm rectangular vents were more successful in catching legal lobsters than traps with smaller vents or no vents.

TABLE 2.—Comparison of commercial catches of sublegal and legal-sized lobsters caught in traps with 58-mm circular vents and traps without vents.

Trap type	No. of sublegals/ trap haul	No. of legals/ trap haul	No. of trap hauls	Sublegals: legals
Side vent:				
double opening	0.98	0.56	144	1.8:1
No vent	2.33	0.49	132	4.7:1
End vent:				
single opening	1.80	0.72	144	2.5:1
No vent	2.76	0.57	144	4.9:1

Possible explanations for these disparities in efficiency may be that: 1) larger lobsters are less likely to enter traps containing several other lobsters, and/or 2) after legal lobsters are caught, their attempts to escape might be intensified as the density of lobsters increases within the trap.

Aside from the previously mentioned differences in the number of shorts caught per trap haul for vented and nonvented traps, end vents (single hole) captured 1.80 shorts/trap haul, whereas side vents (double hole) caught only 0.98 shorts/trap haul (t-test, $P<0.01$). Apparently, the additional vent will insure greater escapement.

Crabs in Research Gear

Since male *C. irroratus* attain larger sizes than females (Krouse 1972), commercial catches of this species are comprised almost entirely of males, so in the following analyses only catches of male crabs are considered. Variations in size composition of catches with different vents as manifested by width-frequency histograms (Figure 3) and mean carapace widths which are statistically different (Duncan's new multiple range test, $P<0.01$) indicate that: 1) fewer large crabs (≥90 mm CW) were captured in traps with horizontal vents (mean 91.2 mm CW); and 2) as many, if not more, larger crabs were collected with circular (mean 96.5 mm CW) than nonvented traps (mean 93.8 mm CW). According to this data, the 58-mm circular vent is at least as efficient in retaining marketable-sized crabs as the nonvented trap and certainly much more efficient than the horizontal vent. Escapement of subcommercial-sized crabs through circular openings has long been recognized by west coast States with Dungeness crab fisheries (Miller 1976). These states require crab traps to have one or two escape rings with diameters ≥4 in.

This situation was further evaluated by comparing the numbers (crabs ≥90 mm CW) per trap haul

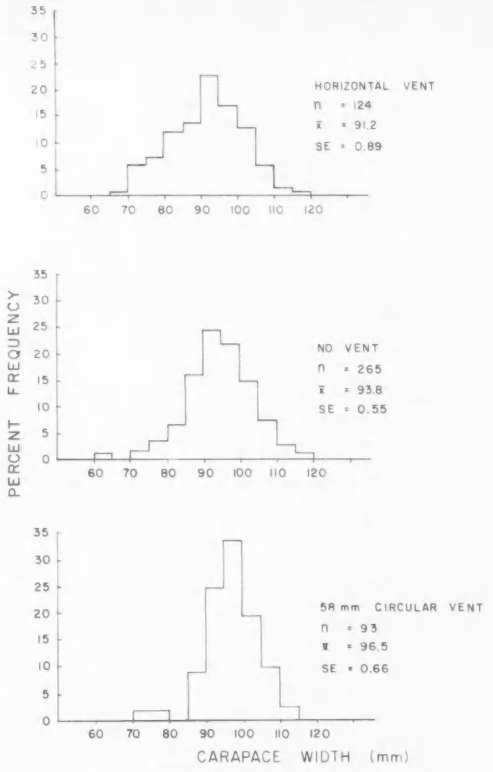

FIGURE 3.—Width-frequency distributions for male rock crabs caught with nonvented traps, traps with 58-mm circular vents, and traps with horizontal vents fished near Boothbay Harbor, Maine.

set over day for each of the different vents (Figure 4). CPUE values were highest for circular vents, lowest for horizontal vents, and intermediate for vertical and nonvented traps. Thus circular vents relative to the other vents were most effective in retaining crabs ≥90 mm CW and based on the following ratios of nonkeepers (<90 mm CW) to keepers (≥90 mm CW), selectively fished for larger crabs:

	Vent type			
	Circular	Nonvented	Horizontal	Vertical
Nonkeepers:keepers	1.5:1	2.5:1	4.1:1	5.7:1

Even though smaller crabs can egress quite readily from traps with horizontal and vertical vents, the above values at first glance appear to reflect the converse, i.e., more nonkeepers are caught in

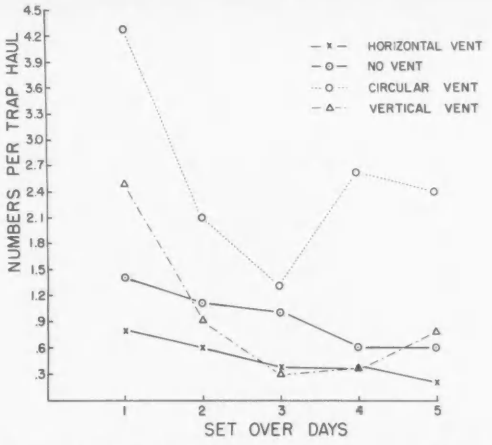

FIGURE 4.—Comparison of the number of rock crabs (≥90 mm carapace width) per trap haul set over day captured with nonvented and circular and rectangular (horizontal and vertical) vented lobster traps.

horizontal and vertical vented traps than in the circular and nonvented traps. Actually, horizontal and vertical vents, unlike circular and nonvented traps, also permit harvestable crabs to escape, resulting in reduced catches of keepers. Consequently, the proportion of nonkeepers to keepers is markedly greater for horizontal and vertical holes.

As evidenced by the aforementioned catch data, selectivity features of horizontal and vertical rectangular vents are similar; however, compared to circular vents they are unsatisfactory for catching large crabs. Prior to field testing, guided by opinions of some fishermen and our own thoughts, it seemed plausible that a vertically positioned rectangular opening (Figure 1A) might inhibit escapement of those crabs with carapace length exceeding the vent's width (smallest dimension). Of course, this was predicated on the assumption that when a crab encounters such a narrow upright opening it will only attempt to egress in a horizontal plane and will not tilt the body diagonally. However, laboratory observations and size composition of catches in traps with vertical vents indicate crabs will readily turn on end or side to exit.

Prior to this, only escapement through the vent itself has been discussed; this certainly does not preclude escapement through entrance heads. Diminishing CPUE values plotted against set over days in Figure 4, particularly for circular and nonvented traps where escapement could only result via the entrances, vividly demonstrate the crab's ability to escape as trap soak time is increased. Evidently, after the voracious crabs become satiated by eating the trap's bait, which frequently occurs in 1 or 2 days during the summer, the trap loses its attractiveness and crabs try to escape. Therefore, crab fishermen can maximize their catches by hauling their traps daily, particularly during periods of high catches. Contrasted to declining crab catches with greater soak times are lobster CPUE values which increase until 4 or 5 set over days, after which catches begin to diminish (Figure 2). Similar trends in CPUE data for commercial catches have been reported by Thomas (1973). Thus it appears that crabs are more adept at escaping from traps than lobsters.

Escapement and Morphometric Studies

Lobsters

Passage of lobsters through a round hole is related to the lobster's carapace height (greatest cross-sectional dimension) relative to hole diameter. Figure 5 shows that: 1) most legal-sized

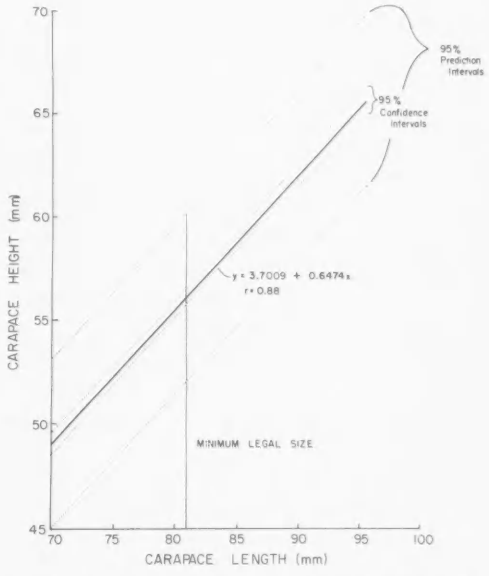

FIGURE 5.—Carapace length-carapace height relationship for lobsters with 95% confidence and prediction intervals.

lobsters with 81 mm CL had <58 mm CH; 2) about half those lobsters with 84 mm CL had <58 mm CH; and 3) lobsters ≥90 mm CL had ≥58 mm CH. Based on this relationship alone, it appears that many lobsters ranging from 81 to 89 mm CL would be able to squeeze through a 58-mm diameter hole; however, this is refuted by the previous sections on the commercial and research catches of lobsters with circular vented traps and the following discussion of escapement studies. Lobster escapement through a round opening cannot be accurately determined by carapace height alone since this measurement excludes the walking legs which contribute to the lobster's overall height or depth. Whether or not a lobster is successful in passing through a round hole will be determined not only by the lobster's greatest transverse dimension (carapace height plus protruding legs) but also by the lobster's ability to maneuver through a tight opening.

Obvious limitations with the aforementioned morphometric relationship caused me to seek an alternate approach to assess escapement. Thus, I decided to determine the largest size lobster that could be manually passed through a 58-mm diameter hole. Lobsters 81 mm CL passed through the hole rather easily following careful manipulation of the walking legs and 82-mm CL lobsters required considerable force, often causing bodily harm, while larger lobsters (>82 mm CL) could not pass through the opening.

Patterns of escapement for lobsters ranging from 78 to 84 mm CL from traps with 58-, 60-, and 61-mm diameter vents varied decidedly as depicted by retention curves in Figure 6. Only the 58-mm vent retained all legal-sized lobsters and still had reasonably high escapement of sublegals; whereas, the other vents which were merely 2 or 3 mm larger allowed legal-sized lobsters to escape. These data emphasize the importance of accurately producing the 58-mm opening, else the vent's desired effect will be lost.

Crabs

Carapace width-length relationships for *C. borealis* and *C. irroratus* graphically show that crabs ≥90 mm CW (commercially harvested size) have carapace lengths (dimension limiting escapement) which exceed 58 mm (Figures 7, 8). Accordingly, commercial-sized crabs of either species cannot egress through a circular opening 58 mm in diameter. In fact, if the vent diameter were increased to as large as 65 mm (certainly, an over estimate) to accommodate an upward shift in the lobster minimum size (Maine Department of Marine Resources recommends an increase from $3^3/_{16}$ to $3\frac{1}{2}$ in CL by $^1/_{16}$-in increments annually over a 5-year period) this would have little or more likely no effect on catches of marketable crabs.

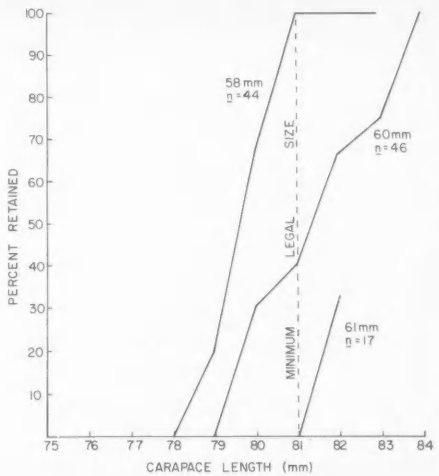

FIGURE 6.—Retention curves for lobsters placed in lobster traps with circular vents of 58, 60, and 61 mm in diameter.

RECOMMENDATIONS

In view of the findings of this study and past investigations (Krouse and Thomas 1975; Krouse 1976), all lobster and crab traps fished in Maine waters should have a rectangular escape vent not less than 1.75 in (44.5 mm) by 6 in (152.4 mm) or at least two circular escape vents not less than 2.28 in (58 mm) in diameter. To insure maximum escapement of sublegal lobsters, vents should be installed next to the sill on the side or end of the trap's parlor section.

Although fishermen should certainly have the option to fabricate their own vents, provided that the prescribed dimensions are adhered to, the use of synthetic, prefabricated vents is highly recommended (Krouse and Thomas 1975). Recently, a plastics manufacturer assured me that vents could be produced and retailed for about 20¢ each. At this low price and with today's high price of laths (about 5¢ each), if a synthetic vent replaces two laths every 3 yr, then after 6 yr the original cost of

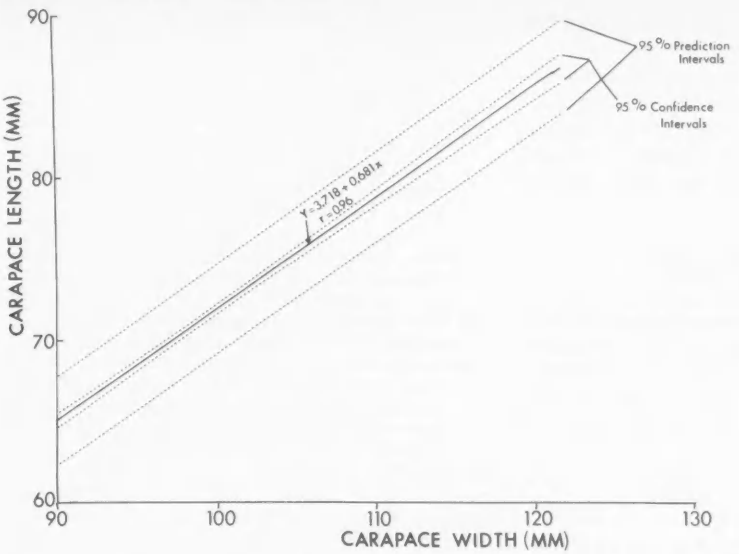

FIGURE 7.—Carapace width-carapace length relationship for male rock crabs with 95% confidence and prediction intervals.

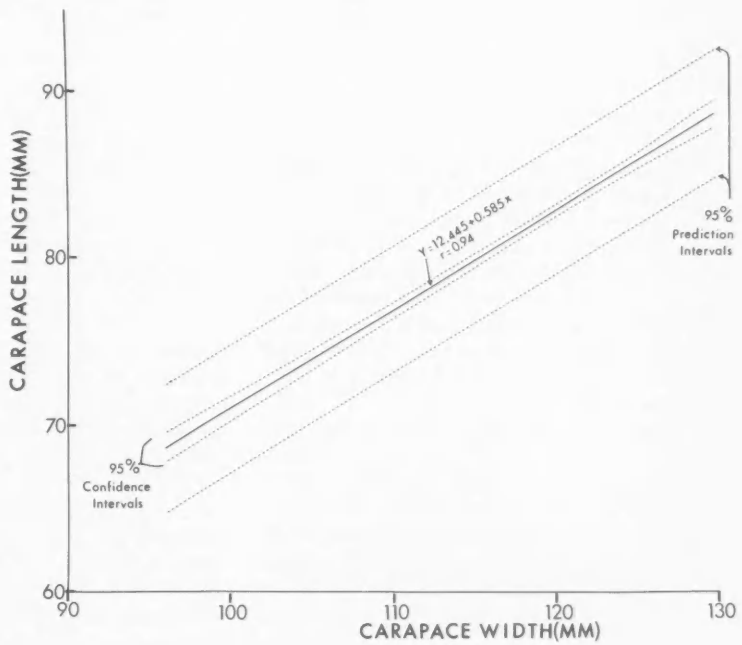

FIGURE 8.—Carapace width-carapace length relationship for Jonah crabs with 95% confidence and prediction intervals.

the vent will be defrayed by the replacement cost of the laths, resulting in a cost savings.

Therefore, those fishermen interested in capturing only lobsters and, perhaps, minimizing their crab catches, would be encouraged to use rectangular vents, while fishermen interested in both lobsters and crabs or solely the latter should employ circular vents.

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SCHOOL STRUCTURE OF THE SQUID *LOLIGO OPALESCENS*

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ABSTRACT

The squid *Loligo opalescens* forms schools which are similar in many respects to those of obligate schooling fishes. These schools are marked by parallel orientation of individuals and strong cohesiveness. Laboratory experiments indicate that the main sensory modality regulating schooling is vision. Squid on opposite sides of a clear rigid Plexiglas barrier readily schooled. The structure of schools of six squid depended on size of individuals and was modified by environmental disturbance. Parallel orientation was weaker in schools of smaller squid (ca. 7 cm dorsal mantle length) than it was in larger ones (ca. 12 cm). In the field, *L. opalescens* schools are composed of uniformly sized individuals. Laboratory experiments designed to determine whether this was due to actual size selection were inconclusive, but they did suggest mechanisms which might be important in determining squid position in the school.

Considerable effort has been spent in understanding the schooling behavior of fish in terms of physiological mechanisms and possible survival value and ecological consequences. (See reviews by Radakov 1973 and Shaw 1970, 1978.) Virtually no work has been done on schooling behavior of invertebrates which occur in the same environments as schooling fish. The most evident schooling invertebrates in the pelagic environment are the squid. Squid and fish play very similar ecological roles and the two groups of organisms possess a large number of similarities. (See Packard 1972, for a discussion of convergent evolution.)

Loligo opalescens is common off the west coast of North America with a reported range from Baja California to lat. 55°N (Fields 1965; Bernard 1970). Relatively little is known of the behavior or general ecology of *L. opalescens* in spite of the fact that there is a fishery for this species in California. The fishery is based primarily upon the tendency of squid to spawn in large aggregations in shallow water (McGowan 1954; Fields 1965). Very little is known about the distribution or location of newly hatched squid as well as squid in later stages of life. Attempts to catch the juveniles have often been unsuccessful (Okutani and McGowan 1969) and only recently have attempts been made to catch nonspawning adults. Even though field data are difficult to obtain, it is possible to keep both juvenile (Hurley 1976) and adult *L. opalescens* alive in the laboratory. Schooling in the laboratory was examined to provide insights about the function of schooling in squid.

METHODS

The squid used in the behavioral studies were obtained either by dipnetting them after they had been attracted to an underwater light or by purchasing them from a local bait dealer. In the laboratory, the squid were maintained in a 3-m diameter circular tank with rapidly circulating seawater. They were fed irregularly on small fish (either mosquitofish, *Gambusia affinus*, or goldfish, *Carassius auratus*). Mosquitofish were taken much more readily than were the goldfish. Occasionally, the squid could be trained to take dead food. This was accomplished by first getting them to accept live fish and by then throwing dead fish in along with the live ones. In this manner, the squid could also be coaxed to accept pieces of frozen northern anchovy, *Engraulis mordax*. If the squid were undamaged when they arrived at the laboratory and there was an abundant supply of small fish available, it was relatively easy to keep them for over a month.

Experiments designed to examine various aspects of schooling behavior were run in a 2 × 3 m rectangular Plexiglas[2] tank which was filled to a depth of 0.4 m. The tank was painted flat white and the primary source of lighting (in addition to general room illumination) was provided by

[1]Moss Landing Marine Laboratories, P.O. Box 223, Moss Landing, CA 95039.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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fluorescent lights placed around the perimeter of the tank which shone through the walls. This provided even, diffuse light in the tank. The water in the tank was noncirculating.

Schooling behavior was recorded on Tri-X film using a 35 mm camera with motor drive and a variable setting automatic timer. A mirror was placed above the tank and pictures were taken of the squid by photographing the surface image reflected in the mirror. A black plastic barrier surrounded the experimental tank. A small hole in the barrier allowed observations to be made of the squid without disturbing them. Exact methods, timing of pictures, etc. varied with the experiment and will be described in the appropriate section.

After the films were developed, they were analyzed using a Scientific Data Products data tablet (Graf-Pen) coupled with a PDP 11-45 computer. The data tablet is a set of microphones placed at right angles which record the sound produced by an electrical spark made by a special marking pen. The x and y coordinates of a point were relayed to the computer by pressing the pen down on the tablet at that point. This device allowed the recording of large amounts of squid position data. In each frame, the tip of the tail, the tip of the outstretched arms, and a point midway between the two eyes were recorded for each squid. Other information, such as the position of barriers, was recorded in the same way. Measurements taken from the photographs were subsequently converted to real distances by multiplication by appropriate scale factors.

Students of schooling have examined school geometry both as a two-dimensional system on a horizontal plane (Breder 1959; Williams 1964; John 1964; Hunter 1966, 1968; Van Olst and Hunter 1970) and as a three-dimensional structure (Cullen et al 1965; Symons 1971a, b; Pitcher 1973). Since squid schools do have a three-dimensional structure in nature, a three-dimensional analysis will eventually be necessary to determine all of the structural details of the school. A three-dimensional analysis, however, is much more difficult than a two-dimensional analysis. It was felt that a two-dimensional analysis would suffice to examine certain aspects of squid schooling behavior. In these experiments, the squid were very nearly confined to a two-dimensional plane by the shallow water depth in the experimental tank. Observations of small schools (up to six squid) in a deeper tank (1 m depth) indicated that the two-dimensional structure observed in the experimental tank was not uncommon.

Three indices were chosen to quantify the angular orientation of individuals in a school, the overall shape of the school, and the distance between neighboring individuals in a school. These indices were proposed by Hunter (1966) and he includes a detailed discussion of their properties. The three indices are:

1. Mean separation distance: An average of the horizontal distances separating each squid from every other squid in the school. It is influenced by school shape, distance between neighboring squid, and number of squid in the school. Distances between all possible pairs of squid are measured and these values are averaged. Distance is measured between the two closest points on the midline of the bodies (including outstretched arms) of the two squid.

2. Mean distance to nearest neighbor: An average of distances from each squid in the school to its nearest neighbor. The measurement is made between the two closest points on the midline of the bodies (including outstretched arms) of the two squid. The same measurement is used twice if two squid are closer to each other than to any other squid.

3. Mean angular deviation: This is a measure of the differences in orientation among squid within a school. The heading of each squid is determined and the resultant direction of the school is computed by assigning each squid a value of one and adding the headings vectorally. The mean number of degrees individual squid deviated from this resultant direction of the school was calculated as the index of orientation.

One difference between squid and most of the schooling fish which have been studied is that squid readily swim both forward and backward. Thus, a squid with an orientation that was 180° out of phase with the rest of the school might still be swimming with the rest of the school. For this reason, one orientation measure was calculated which regarded the squid as a line segment rather than as a directed vector and measured the smallest angular deviation between line segments. Such measurements were rarely different from measurements made considering the orientation of the squid and therefore will not be considered further in this paper.

Where measurements of squid length are given, they are of dorsal mantle length from tip of the pen to the tip of the tail. The total length of the squid (including arms but excluding tentacles) is about 1.3-1.5 times the dorsal mantle length (Fields 1965).

RESULTS

Response to Disturbance

One set of factors that caused changes in schooling can be grouped under "external disturbances." These included introducing objects (such as a net) into the water near the squid or tapping on the side of the tank. The typical response was for the squid to group more tightly and, in cases where it was not already marked, to increase the degree of parallel orientation. The amount of change in schooling behavior and the temporal characteristics of this change depended upon the nature and intensity of the disturbance and upon its duration.

One attempt at quantifying the stimulus involved placing an aquarium air stone in the tank. Pressurized air delivered to this air stone in differing amounts and duration produced a stream of bubbles which could be used as a disturbance stimulus of varied intensity and duration. A small stream of bubbles produced little squid reaction, while vigorous water action due to the bubble stream produced marked changes in behavior. Figure 1 shows the changes in three of the schooling indices in response to a moderate disturbance caused by turning on the air bubble stimulus. The degree of parallel orientation, which was already pronounced, did not change appreciably. But the squid did draw noticeably closer together.

Schooling Structure as a Function of Squid Size

Six squid of nearly equal size were haphazardly taken from the holding tank and placed in the experimental tank. The squid swam in this tank for an hour before measurements were made. With the exception of one experiment, a picture was taken of the squid every minute for approximately 1 h. During this other experiment, a picture was taken every 10 s for 10 min. This set of experiments was conducted during the daylight hours of two different days. All of the squid used in this set of experiments had been captured on the same night.

There was a decrease in the mean angular deviation as the size of the squid increased (Table 1). Since small values of the mean angular deviation index are associated with increased parallel orientation, the degree of parallel orientation is greatest in schools composed of large individuals. Even in the case of the small individuals, however, the value of the index does not approach what would be expected if the squid were each orienting in a random direction. In a simulation of 1 million values for six randomly oriented fish, Hunter (1966) found that the mode of the frequency distribution was 69°.

Although the average values for mean angular deviation do give a measure of average departure from parallel orientation for a whole experiment, they do not give an indication of how variable a particular group of squid is in its orientation over time. For example, an experiment of 30 pictures and an average value of the mean angular deviation index of 20° could have had all of the 30 values close to 20°. This would indicate a consistent moderate degree of parallel orientation over time. On the other hand, such an average value could also come from a situation where the squid had strong parallel orientation part of the time and were much more loosely oriented the rest of the time (e.g., the index value could have been 10° on 15 frames and 30° on 15). This kind of difference can be detected if a measure of the variability of the mean angular deviation index for each experiment is calculated. The variability (standard deviation, SD, Table 1) increased with decreasing squid size, indicating that not only do the smaller squid not orient on the average in as parallel a manner as larger squid, but they are also more temporally variable in their orientation. This difference can also be seen if individual experiments are examined. Figure 2 shows the values for mean separation distance and mean angular deviation

TABLE 1.—Relationship between average size of *Loligo opalescens* and parallel orientation and separation of individuals in the six-squid experiments. Each index was calculated for each frame.

Group number	Mean mantle length (cm)	No. frames examined	Mean angular deviation index (degrees)		Mean separation distance index (cm)	
			$\bar{x}$	SD	$\bar{x}$	SD
1	7.5	44	32.0	18.4	32.3	26.5
2	7.6	58	29.0	15.3	25.6	8.0
3	7.7	60	18.1	10.7	16.2	4.5
4	9.7	19	18.5	5.7	14.0	4.2
5	9.7	62	16.2	6.2	18.7	5.2
6	10.2	69	17.2	6.6	20.9	5.0
7	11.9	65	11.1	5.6	18.5	4.0
8	12.0	55	9.6	2.8	15.3	2.7
9	12.0	46	9.1	4.2	13.8	3.0

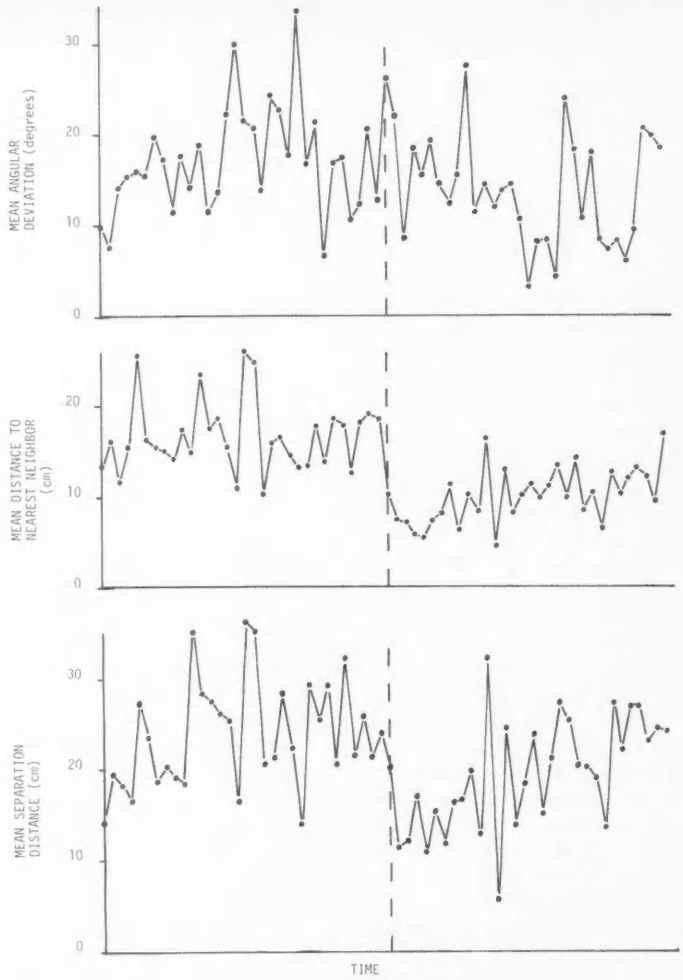

FIGURE 1.—Values of schooling indices for a school of six *Loligo opalescens* before and after disturbance (turning on bubbler). Dashed line indicates when air was turned on. Pictures were taken every minute for 64 min.

for two (Groups 3 and 7) of the experimental runs summarized in Table 1. The parallel orientation is stronger and the variability less in the larger squid (Figure 2C, D). The mean separation distance index is not as clear a function of size (Table 1; Figure 2A, B).

Schools in the Ocean

Very little is known of the natural behavior of *Loligo opalescens* when it is not in large mating schools. In many areas, there often is a large concentration of squid in the vicinity of the deep-scattering layer (C. Recksiek, Moss Landing Marine Laboratories, Moss Landing, CA 95039, pers. commun., October 1976) and large layered concentrations of *L. opalescens* have been reported by those involved in submersible exploration (A. Flechsig, Sea Grant Marine Advisory Service, University of California at San Diego, La Jolla, CA 92093, 1973). There is evidence to indicate, however, that *L. opalescens* is often found in much smaller schools and that these schools contain a narrow size range of individuals. Fields (1965) presents data on the uniformity of size of young squid taken from the same fish catch (presumably the same squid school) and speculates that the size ranges in the schools he observed represent approximately one-half or less than one-half of a year's growth.

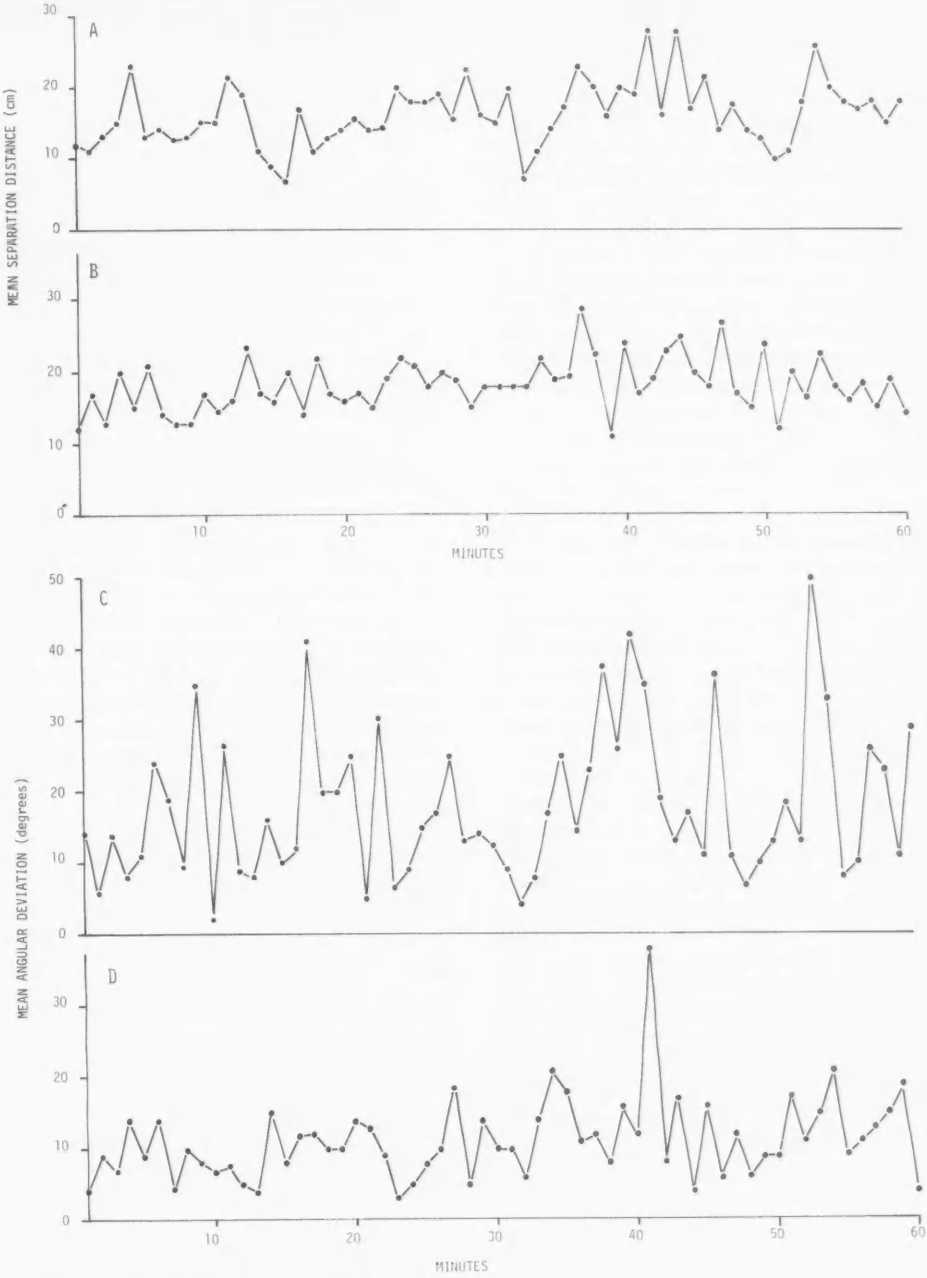

FIGURE 2.—Values of mean separation distance and mean angular deviation for two (Groups 3 and 7) of the experiments presented in Table 1. Mean size of *Loligo opalescens* in the experiment represented in A and C was 7.7 cm mantle length. Mean size of squid in the experiment represented in B and D was 11.9 cm mantle length.

I also obtained data on the uniformity of size in individuals of the same school. The squid were caught during a 1-wk period in August in locations ranging from San Diego to Santa Catalina Island, Calif. A night-light was placed off the stern of the ship in the center of an L-shaped 3-m long mesh net. Squid were attracted to the light and would rush into the net. The net was then raised and the squid could be removed with dip nets. The "schools" were all of the squid which swam into the net at the same time. Squid caught during this period ranged from 5.8 to 17.3 cm dorsal mantle length. But for a given school, they were much more uniform in length. The average size range for 29 schools of 2 to 32 individuals was 2.5 cm.

Maintenance of School Structure and Orientation

Experiments in the laboratory have indicated that vision is sufficient sensory input to mediate schooling behavior. Squid on different sides of a clear, rigid Plexiglas barrier will readily school with each other and they appear to maintain the same type of parallel orientation that is present in normal schooling behavior. Preliminary experiments using such Plexiglas barriers were run to try to elucidate the mechanisms by which spacing is maintained.

Two-Squid Experiments

Experiments were run to determine whether squid would school in the same manner with or without a clear Plexiglas barrier in place. Measurements were obtained for squid swimming together and for the same squid swimming on opposite sides of a Plexiglas barrier which divided the tank into two compartments. The order of the treatment was randomized for each pair of squid. Squid ranged in size from 7 to 13 cm mantle length. For a given experiment, the two squid were of similar length. Pictures were taken of the squid in each treatment every 10 s for 3 min after they first came together and again every 10 s for 3 min after the squid had been left undisturbed for 15 min. If the squid did not come together to within at least 0.5 m within 1 min, the experiment was terminated.

Table 2 shows the results of five such experiments. The first 3-min periods have been compared with each other, as have the later runs. This was to see if the pattern of schooling changed after the squid became more adapted to the experimental regime. This table presents results for the median nearest distance between the two squid for each run and for the median separation angle for these same runs. Separation angle for each frame is simply a measurement of the angle between the two squid and is a measure of orientation (0° separation angle indicating parallel alignment facing the same direction).

TABLE 2.—Median nearest distances and median separation angles for two-squid (*Loligo opalescens*) experiments.

Item	With barrier	Without barrier	Difference[1]
Nearest distance (cm) first 3 min	20.6	16.2	$P = 0.05$ barrier greater
	11.3	6.6	$P < 0.01$ barrier greater
	38.6	11.65	$P < 0.01$ barrier greater
	14.9	7.9	$P < 0.01$ barrier greater
	13.8	6.4	$P < 0.01$ barrier greater
Nearest distance (cm) second 3 min	24.2	15.8	$P < 0.01$ barrier greater
	18.4	6.3	$P < 0.01$ barrier greater
	23.9	18.35	$P < 0.05$ barrier greater
	14.35	13.1	$P < 0.05$ barrier greater
	12.5	8.2	$P < 0.01$ barrier greater
Separation angles (degrees) first 3 min	16.4	52.7	$P < 0.01$ barrier less
	24.3	11.2	$P < 0.05$ barrier greater
	75.1	21.0	$P < 0.01$ barrier greater
	21.2	12.2	NS[2]
	17.0	30.9	$P < 0.05$ barrier less
Separation angles (degrees) second 3 min	28.2	15.4	$P < 0.05$ barrier greater
	15.4	13.6	NS
	19.1	18.0	NS
	25.4	18.3	NS
	11.1	24.9	$P < 0.05$ barrier less

[1]Significance of difference in medians from Mann-Whitney *U*-test.
[2]NS = no significant difference, $P > 0.05$.

The barrier has an effect upon the separation distance between the two squid. In all cases, there was a significant difference between the distance between squid with and without the barrier. When the Plexiglas barrier was present, the squid tended to space themselves farther apart. There is not a clear relationship between angular separation and the presence of the barrier. Of the six runs showing significant differences, three had greater median separation angles with the barrier in place and three had greater median separation angles when the barrier was not present.

Three-Squid Experiments

The experimental tank was divided crosswise into three equal compartments (1 × 2 m each) by clear Plexiglas partitions. A squid was chosen from the holding tank and was placed in the central compartment. Then a squid for each of the outer compartments was selected. These squid were assigned at random to each of the outer compartments. The squid were allowed to adapt to the experimental situation for 15 min and then were filmed for 5 min (one picture every 10 s). The two

outer squid were then switched from one outer compartment to the other and the squid were again allowed to adapt for 15 min. They were then filmed for 5 min (once every 10 s). Squid in these experiments ranged from 9.2 to 15.3 cm mantle length.

It was hoped that this experimental design would indicate whether the center squid, if given a choice, would choose to school with a larger or smaller squid or one closer to its own size. One way to determine whether such a choice is being made would be to determine whether the center squid spends more of its time closer to one outer squid than to the other. Each 5-min run was considered as a unit and each frame was scored according to which outer squid the center squid was nearest. For each run, the data were compared with a binomial distribution which assumed that the center squid had an equal probability of being closest to either outer squid. Of the 17 runs, 16 showed a significant deviation from the expected binomial distribution ($P \leq 0.05$ for 1; $P \leq 0.01$ for 15). These 16 runs were now grouped according to whether the center squid was closest to the larger or smaller outer squid. In 8 of the 16 cases, the center squid was nearest the larger outer squid, while in the other 8 cases, it was nearest the smaller squid. There is no evident preference for large versus small squid. The data can also be arranged to determine whether the center squid spent most of its time near the squid closer to its own size. There were 14 runs for which it was possible to say that the center squid was closer in size to one of the outer squid. Of these 14 runs, the center squid was significantly nearer to the squid closer to its own size 9 times and nearer to the squid farther from its own size 5 times.

These experiments may be viewed in another way by looking at the absolute position of the squid in the tank. The nearest distances of the squid to the Plexiglas barriers were calculated for each frame. These data are summarized in Figure 3 for the 17 runs. The side squid usually are very near the barrier which separates them from the center compartment, while the center squid varies his position within the center compartment, but approaches the Plexiglas barriers much less often.

DISCUSSION

Pelagic fish and squid represent a striking case of convergent evolution, not only morphologically (Packard 1972), but behaviorally as well. One aspect of behavior where this is particularly apparent is schooling. Since many of the same ecological pressures exist for both pelagic groups, it is not surprising that some sort of schooling behavior would have developed in both fish and squid. What is surprising, given the very different physiology and mode of locomotion, is that so many aspects of this behavior are the same.

Loligo opalescens fits Breder's (1967) definition of obligate schoolers. Single *L. opalescens* are rarely caught in the field, and they immediately come together when placed in a tank in the laboratory. As has been reported for many species of fish (Radakov 1973), *L. opalescens* schools consist of individuals of approximately the same size. It has been suggested that the reason that fish school in such groups has to do with swimming speed. Small and large individuals would not swim at the same speed and thus would not normally stay together. This is possibly also true for squid, but data on the swimming speed of large and small *L. opalescens* are not available to substantiate the argument. For several reasons, the swimming speed hypothesis seems less plausible for squid than for fish. In schools of fish which show parallel orientation, the fish continually maintain forward motion and thus swimming speed is likely to be an important factor. But field and laboratory observations have indicated that individuals in squid schools spend much of their time hovering in the same position in the water column with only

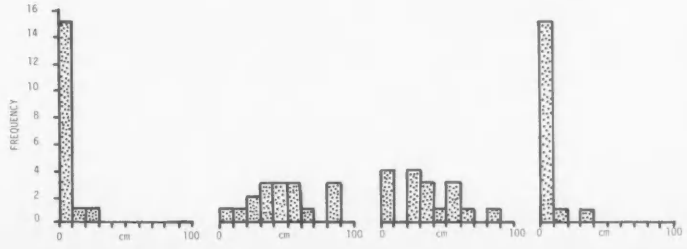

FIGURE 3.—Histograms of mean nearest distance between *Loligo opalescens* and barrier in the 17 three-squid experiments. Distances are broken up into 10-cm intervals. From left to right: left outer squid to left barrier, center squid to left barrier, center squid to right barrier, right outer squid to right barrier.

slight backward and forward motion caused by jets of water from the siphon. Even when disturbed, the squid do not make long extended swims which would tend to sort out those of differing swimming ability. In the field, the most common response of a squid school to a disturbance (the presence of a scuba diver or a shark) is to clump closer together and move off a slight distance. On one occasion when I was diving in a large spawning school (several thousand individuals), the squid executed the same type of maneuver that has been reported for fish schools. Instead of moving off, the school completely enclosed me, leaving a spherical space of approximately 3 m radius around the "predator."

One other piece of evidence suggests that it is not differences in swimming speed alone which cause the squid to school according to size. While diving in the Bahamas in the Hydrolab underwater habitat, we observed a school of squid which routinely visited the habitat. This school was composed of *Doryteuthis plei*, a species which quite closely resembles *L. opalescens* and presumably has similar swimming ability. This school consisted of seven squid and, in this case, was not composed of individuals of the same size, the largest individual being at least two times the length of the smallest individual. We chased this school several times but were never able to force them to separate. The smallest squid maintained the same swimming speed as the largest squid.

It is possible that squid maintain schools of individuals of a fairly narrow size range because of social factors. Generally, workers studying schooling have assumed that all of the fish in a school may be treated as equivalent individuals in the production of the behavior and that there is no social structure in the schools. In fact, some workers have suggested that schooling is really just a modified form of individual cover-seeking behavior (Williams 1964; Hamilton 1971). This assumption of equality of individuals may be an untenable one for squid schools. In the field, Hochberg and Couch (1971) observed signaling by some members of a school of *Sepioteuthis sepioidea* which they felt prevented other squid from joining the school. Furthermore, in the laboratory, I have observed complicated agressive interactions in *L. opalescens* which certainly demonstrate that all squid cannot be considered behaviorally equivalent individuals at all times (Hurley 1977).

One aspect of schooling in fish which has been emphasized by many workers is that the structure of schools may change as a function of the age or the physiological condition of the fish. Van Olst and Hunter (1970), for instance, found that in five species of marine fishes, schools of young fish were less compact and showed greater differences in angular headings than did schools of adult fish. In addition, Hunter (1966) showed that distances between jack mackerel tended to increase with food deprivation, while Keenleyside (1955) noticed that sticklebacks were more densely packed in a school when well fed than when starved.

I attempted to determine whether similar phenomena were observable in squid schools. Schools of small squid (7-9 cm mantle length) gave the impression of being less cohesive than schools of larger squid (13-15 cm mantle length). This was supported to some extent by the quantitative measurements, particularly those of angular orientation. The variability was also higher for all of the indices for the smaller squid. It has been suggested for fish (Van Olst and Hunter 1970) that the observed change with size could have been an adaptation to the higher food requirements of the juvenile fish. This speculation is supported by observations that a number of species school less cohesively under conditions of food deprivation. The same explanation may also hold for squid, but my existing data do not support it. I ran two experiments in which schools of six squid were filmed before and after feeding. In one experiment, there were no significant differences in the schooling indices before and after feeding, while in the other, there was significantly less school cohesion and parallel orientation after feeding. In any event, it is not possible to guess which factors are instrumental in this increased cohesiveness and consistent geometry.

As is the case for fish, vision seems to be the primary sensory system used in squid schooling. Squid will readily school across a clear, rigid Plexiglas barrier, although they tend to stay somewhat farther apart than they normally would. Investigators dealing with fish also found that the presence of a clear, rigid barrier caused abnormalities in the spacing between individuals, in some cases increasing the fish-to-fish distance (Cahn 1972) and in some cases decreasing it (Shaw 1969). These workers speculated that this change was due to lack of lateral line input and a resultant loss of information concerning the position of the adjacent fish. Squid do not have a similar extensive vibration-sensitive system, although they may be able to detect vibrations with their stato-

cysts. In the case of *L. opalescens*, the most likely explanation for this change in spacing is that the presence of the barrier physically limits the extent to which each squid can compensate for the other individual's movements. In the experimental tank, squid seemed to differ in their motivation to school. When the barrier was not present, a squid with a strong tendency to school could always maintain proximity to another squid. But if the barrier were present, that squid could only follow another squid as far as the barrier and had to remain there until the other squid returned.

I had hoped that the experiments with the three squid separated by Plexiglas barriers would give some clue as to whether the squid actively chose to school with individuals of the same size, but the results were inconclusive. The results did indicate, however, a possible mechanism for maintenance of spacing within a school. The center squid tended to stay toward the middle of the compartment, while the side squid maintained positions very near the Plexiglas barrier. It is possible that the center squid was attempting to equalize the visual angle subtended by the squid on each side, while the outer squid were attempting to get into positions with squid on each side. The measurements of visual angle which I can get from my photographs are not accurate enough to determine whether this is happening. If outer squid are continually trying to achieve a position where they have squid on either side of them, individuals in a school should be continually shifting positions. Casual observations have indicated that this does happen some of the time; but at other times, the individuals maintain the same positions relative to one another.

An area where a comparison of squid and fish schooling may be useful is in the speculation concerning the evolution of the schooling behavior and its possible advantages. Many recent papers have concentrated on the hydrodynamic advantages of fish schooling (e.g., Breder 1976) and base their explanations of many of the details of school structure on the fish mode of tail-flip locomotion and the vortices which are subsequently created. Van Olst and Hunter (1970) suggest that the typical nearest neighbor distance in fish schools is about one-half a body length and that this distance may be explained by considering the amplitude of the tail beat in swimming. It is interesting that in squid, with their very different mode of locomotion (jet propulsion as opposed to tail flips), the spacing between nearest neighbors is still maintained between one-half and one body length in undisturbed squid.

Other investigators have speculated that a primary function of schooling is as a defense against predation. (See reviews by Shaw 1970 and Radakov 1973.) Squid have many of the same reactions to disturbance that fish do. They both clump more closely together as a result of disturbance and both have been seen to surround their predators. Further evidence which suggests that predator defense may be an important function of squid schooling comes from the development of the behavior in juvenile squid. In the course of rearing *L. opalescens* (Hurley 1976), I made observations on schooling behavior. The newly hatched squid appeared to have no attraction to each other, but after 6 or 7 wk schooling was occasionally observed. This schooling was only evident in response to disturbance (tapping on the tank or putting a net into the water). When the squid were feeding undisturbed, there was no obvious schooling behavior.

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NORTHERN ANCHOVY SCHOOL SHAPES AS RELATED TO PROBLEMS IN SCHOOL SIZE ESTIMATION

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ABSTRACT

Horizontal fish school profiles of the northern anchovy, *Engraulis mordax*, taken from day aerial photographs and video tapes of school bioluminescence at night were examined to determine the percentage of school area within a circular field of view and the school length and width ratios. Schools observed during the day had an average length to width ratio of 2.09:1, at night the ratio was 2.53:1. The percent coverage of the school's area in relation to a circle drawn tangent about the school averaged 42.1% during the day and 29.2% during the night. The effect of school shape on estimation of individual school area as observed with a side-looking sonar was determined. School width measurements, similar to that obtained by the sonar, were used to determine school area and indicated a possible average overestimate of the actual school area of 1.72:1. The relation of school length and width to the error was determined, indicating the greater the length to width ratio the greater the error.

Profiles of fish schools as viewed and photographed in the horizontal plane from an airborne platform have been published by numerous authors. Radakov (1972), in his review of fish schooling, described the characteristic horizontal shapes of fish schools in nature as being very diverse and extremely changeable. He stated that a spherical shape of a school is the rarest of all and also that a school's shape, size, or density is a result of the interaction between the fish and the physical and biological environment.

School shape and behavior in nature have been studied with such techniques as aerial observation, hydroacoustic measurements, and underwater observation. Each of these methods has limitations. Underwater visual observations are subject to restrictions due to illumination and restricted visibility. Aerial observation is limited in the day by water transparency, illumination, and reflectance from the water surface resulting from wind and wave action. Visual observation of school shape at night, as outlined by bioluminescent organisms, is limited to the moon's dark cycle or to periods of no moon, and is affected by water transparency and the density of bioluminescent organisms present in the water. Both day and night observations are limited by the school's proximity to the surface in relation to the factors affecting water visibility.

Hydroacoustic observations using lower frequency sounders of the type used commonly in sonar fish surveys give imprecise images of fish schools in the form of echograms that must be interpreted. Greater resolution of fish school shapes, but with limited range, can be obtained with ultrasonic scanning equipment (Voglis and Cook 1966).

All of these observation techniques may alter the environment and in many cases may result in modification of fish school behavior. Fish school behavior is affected when in close proximity to ships, submersibles, and divers, and aircraft (noise, shadow) could possibly modify the school, though this is not documented.

Surveys and research studies using variations of these three observation techniques are currently in use for direct biomass estimation of fish populations by observation of individual schools, school groups, and the internal structure of the school.

Hydroacoustic research on schooling fish is currently being conducted by the Southwest Fisheries Center (Smith 1970; Hewitt et al. 1976). Coastal, hydroacoustic surveys are conducted by the State of California (Mais 1974) to determine a relative abundance estimate of the northern anchovy, *Engraulis mordax*. These surveys are conducted during the daylight hours, as comparative tests indicate an increased probability of detection during this period (Smith 1970).

Aerial observations by commercial fish spotters, in the form of school counts and estimates of total tonnage, are being used by the Southwest

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Fisheries Center to calculate indices of apparent abundance for several coastal species, including the northern anchovy (Squire 1972). To aid in the detection and quantification of pilchard, *Sardinops ocellata*, shoal occurrence off South Africa, Cram (1974) used an airborne, low-light-level, electron image intensifier to view the ocean's surface, detecting the bioluminescence of fish schools. During these night aerial surveys the school's horizontal surface area was interposed on the instrument's circular field of view, and running estimates of the percentage of coverage were made. These percentage estimates were then used in the computation of biomass estimates.

The intensifier used by the Sea Fisheries of South Africa has been used by the author off the southern California coast on an experimental basis. Due to the highly variable school shapes encountered, making estimates of the percentage of school coverage in the circular field of view are difficult. Experience indicated that examination of aerial color photographs and night low-level video tapes of anchovy school shapes for determination of the percentage of school coverage within a circle would be useful, particularly if in the future, surveys were to be conducted at night using this method for the development of biomass estimates for the northern anchovy and other near-surface schooling pelagic species.

In addition, an analysis of anchovy horizontal school shapes may assist hydroacoustic researchers in determining error parameters for computation of sonar biomass estimates. Hydroacoustic surveys currently conducted for the northern anchovy use both side- and vertical-looking sonar to detect and measure fish schools and school groups during the day along a predetermined survey track line. The acoustic "beam" used in these surveys varies according to the unit and is of ±5° to 10°. When detecting the school, the side-looking sonar measures the maximum dimension in one aspect of the school, either normal to or parallel to the ship's track. For the purpose of calculating horizontal area, in contrast to the aircraft's vertical view of the actual horizontal school area, the echogram school width is assumed to be elliptical (Smith 1970). Preliminary attempts at biomass estimation from sonar surveys have used the simple assumption that a series of estimates of the width of an elliptical school from random aspects will result in an unbiased estimate of school horizontal area. In a side-looking sonar the school width is measured and provides two points of reference with the orientation of these points about the school's profile being unknown. If an ellipse is fitted randomly between these two points, the resulting average area will equal a circle, a condition that was not observed in aerial photographs of anchovy schools.

METHODS

To examine the shape of northern anchovy schools as observed during day and night and to determine what percentage the school occupies of a circle tangent to two points along the school's edge and containing the school inside the circle, a circle was drawn about school profiles obtained from a series of 20 day oblique aerial color photographs (from the photographic files of the Southwest Fisheries Center) and of 20 night photographs of fish school bioluminescence. The bioluminescent anchovy school shapes were photographed from a television monitor as it projected video tapes recorded from an airborne low-light-level television camera used during anchovy resource surveys off northwestern Mexico. The night photographs were made available through the courtesy of Zapata, Inc.[2] (Zapata Fisheries), Houston, Tex. The night surveys using low-light-level television were conducted at elevations of up to 1,828 m (6,000 ft) and this survey technique is effective because the northern anchovy commonly migrates to the near-surface area during hours of darkness (Squire 1972).

The actual area of the schools observed in the photographs are unknown due to lack of data on the aircraft's altitude, camera angle, and camera geometry; however, all were taken from angles approaching vertical. However, all area calculations are expressed in percentages of a circle drawn tangent about the school's edge.

The day school profiles were further analyzed to determine what the school area would be if the width measurement were considered to be equal to the school's diameter and what the area would be if viewed systematically from six points 30° arc) about an arc of 180° around the school (based on school width or diameter as determined similar to the measurements made from a hydroacoustic sounder). These area data calculated from the six points of observation to determine school width were then compared to the actual school area.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

School length to width ratios were determined for both day and night schools.

The school area, as expressed in terms of percentage of the circle drawn about it, was determined by tracing the school profile upon paper, cutting the school out of the circle and weighing both the school profile and the nonschool portion of the circle on a sensitive laboratory balance. School areas for the six points of school width (diameter) measurement about the 180° arc were computed statistically.

RESULTS

Night Observations

Figure 1 illustrates the profiles of schools recorded by the airborne low-light-level television system. On each figure are given the area percentage of a tangent circle that the fish school occupies and the length to width ratio.

The average percent coverage of a night anchovy school, in relation to the circle tangent to the school, is 29.2%. The average ratio of school length to width is 2.53:1.

Day Observations

Figure 2 illustrates profiles of schools observed during the day. On each figure are given the percentage of a circle tangent to the school that is occupied by the fish school, the length to width ratio, and the 30° arc points that were used to determine the school's estimated diameter and area, simulated as randomly viewed by a side-looking sonar. The ratio of the actual school area to the calculated area of the school's average, high and low estimate, as viewed every 30° of a 180° arc based on simulated sonar measurements of width, is given in Table 1.

The average percent coverage of a day anchovy school to the tangent circle about the school is 42.1%. The average length to width ratio for all day schools is 2.09:1. The ratio of estimate of the area of all day schools, as calculated from measurements from 30° arc points about the school, to the actual area of the school is 1.72:1. The ratios, length to width, and estimate of school area to actual school area were compared and Figure 3 graphs the relationship. The graph displays the variables plotted on log-log paper showing two main points: One, that the variance is changing proportionally to the mean. This is expected as there should be more variation as the school length to width increases. Two, the plotted regression line indicates that more bias (higher estimated actual school ratio) is introduced as the school length to width ratio increases. The line is significant at the 95% confidence interval as proven by the t-test ($1.98 < 2.298$). The confidence limits are from 0.0545 to 0.734.

TABLE 1.—Ratio of the actual anchovy school area to the average area based on six points of observation as viewed every 30° of a 180° area, and the high and low ratio.

School	Average	High	Low
1D	1:2.61	1:3.95	1:0.83
2D	1:1.96	1:2.91	1:0.90
3D	1:1.22	1:1.56	1:0.85
4D	1:2.12	1:3.71	1:0.63
5D	1:1.13	1:1.41	1:0.80
6D	1:2.73	1:4.53	1:1.18
7D	1:1.50	1:2.35	1:0.60
8D	1:1.32	1:2.00	1:0.54
9D	1:1.49	1:1.88	1:1.19
10D	1:1.31	1:1.60	1:1.04
11D	1:2.65	1:4.82	1:0.62
12D	1:1.33	1:2.02	1:0.85
13D	1:1.47	1:2.35	1:0.77
14D	1:1.68	1:2.54	1:0.49
15D	1:1.97	1:3.30	1:0.65
16D	1:1.60	1:2.69	1:0.44
17D	1:1.38	1:2.10	1:0.84
18D	1:1.38	1:2.00	1:0.68
19D	1:1.99	1:3.52	1:0.42
20D	1:1.77	1:2.90	1:0.66

SUMMARY AND COMMENTS

The data on day/night school length to width ratios support what is commonly known about the schooling shapes of the northern anchovy. They are more common in the near-surface area at night, generally in large elongate thin surface schools. These elongate schools tend to group together in the early morning hours and descend to depth to form more compact schools during the day (Mais 1974). Studies by Squire (1972) of aerial fish spotter data show anchovy schools to be more frequently observed, and observed in larger quantities at night, when compared with day observations.

The schools percent area coverage of the tangent circle at night is 12.9% less than its coverage during the day and the length to width ratio is greater by 0.44. In addition, analysis of school length to width ratios compared to the ratio of estimated school size to actual size (Figure 3) shows that as the length to width ratio increases a greater error in school area estimate will occur. Schools with a length to width ratio of 2:1 have an estimated to actual error of about 1.5:1 while more elongate schools of a ratio of 3:1 have an estimated error of about 1.75:1.

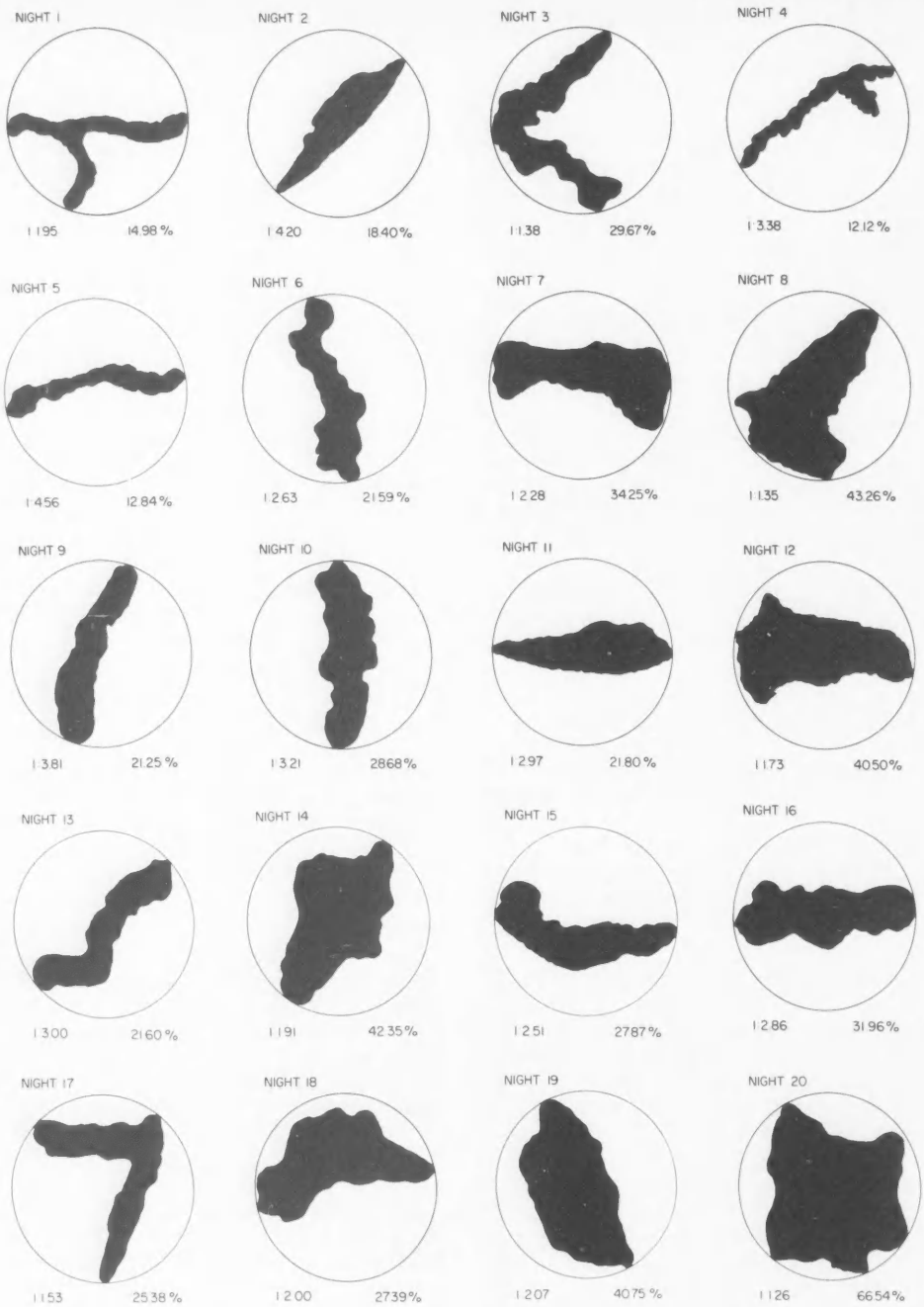

FIGURE 1.—Profiles of anchovy schools observed at night off southern California, indicating the width to length ratio and the percentage of a tangent circle about the school.

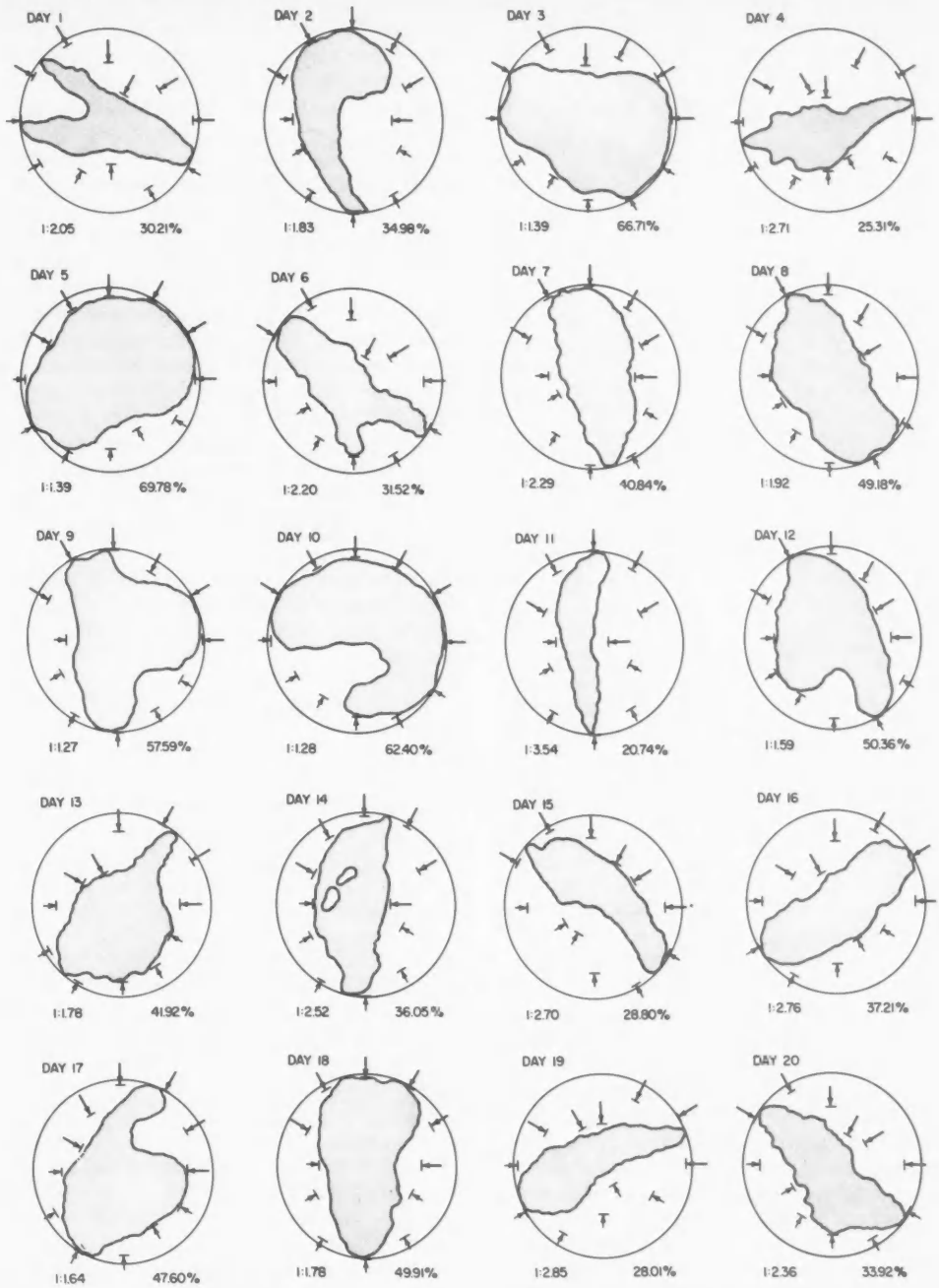

FIGURE 2.—Profiles of anchovy schools observed during the day off southern California, indicating the width to length ratio and the percentage of a tangent circle about the school. Measurements of school width were taken at the six points (long arrow shaft) indicated about a 180° arc.

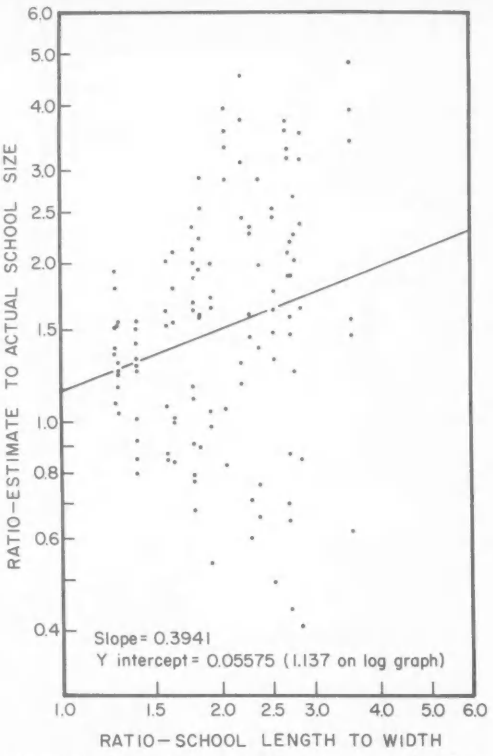

FIGURE 3.—Regression plot for the ratio estimated anchovy school size to actual size compared with the school length to width ratio.

For simulated sonar observations of school widths used in the calculation of school area, the preliminary examination of these data indicates a possible 1.72:1 average overestimate of area due to school shape deviations from a circle or ellipse.

Fish schools, being highly variable in horizontal profile, are probably equally complex in vertical structure; the relationship of horizontal complexity to vertical complexity is not known. Also unknown is the question of whether the individual school's axis is oriented in the same general direction within a group of schools, a possible factor which, if it occurs, could provide a source of substantially higher or lower school area error estimates from sonar track line surveys.

The problem of accurately estimating the percentage of school area within view of a low-light-level viewer is difficult, as the examples of school shapes within the target circle would indicate. Parameters of human viewing error could be established for this survey technique. However, the conduct of surveys using a low-light-level television system where the video signal can be recorded and later electronically analyzed with the aid of an image analyzer, should result in a higher degree of survey accuracy.

School shapes were taken from photographs randomly selected from an aerial photo file. Many of the photos were taken in the nearshore areas. There is the possibility that schools may be slightly more elliptical in shape over deep water than in the nearshore areas, but this is not documented. If this were true the error estimate would be reduced. This and other aspects of school profile and orientation should be investigated further and estimates of length to width ratios from aerial surveys, done in conjunction with each acoustic survey, may be useful for determination of a correction factor for the acoustic data.

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SYNERGISTIC EFFECTS OF ENVIRONMENTAL VARIABLES ON THE METABOLISM OF THE COPEPOD *EUTERPINA ACUTIFRONS* FROM TWO DIFFERENT AREAS OFF THE COAST OF THE STATE OF SÃO PAULO, BRAZIL[1]

G. SOARES MOREIRA[2] AND W. B. VERNBERG[3]

ABSTRACT

The combined effects of temperature and salinity on the respiratory rate of two populations of the copepod *Euterpina acutifrons* have been determined. One population was taken from a nonpolluted area, São Sebastião Channel, and the other from a polluted area, Santos Bay, both off the coast of the State of São Paulo, Brazil. Four groups of copepods were used in the experiments: 1) São Sebastião animals kept in São Sebastião water (35‰ salinity); 2) Santos animals kept in Santos water (28‰ salinity); 3) São Sebastião animals kept in Santos water; and 4) São Sebastião animals kept in diluted São Sebastião water (28‰ salinity). Results showed that São Sebastião copepods in either full strength seawater (35‰) or lower salinity seawater (28‰) could metabolically regulate over a wider range of salinities than could Santos copepods in Santos water or São Sebastião copepods maintained in Santos water. It was concluded that the water quality of the Santos Bay was responsible for changes in the metabolic regulatory capacity of the copepods exposed to Santos water.

The planktonic harpacticoid *Euterpina acutifrons* (Dana) is distributed in the warm waters of the world between lat. 66°N and 40°S (Haq 1972). It is a euryhaline species and has been reported in salinities ranging from 8‰ (Cananeia Estuary, southern Brazil, Tundisi 1972) to 39‰ (Mediterranean Sea, El-Maghraby 1965). Laboratory studies have shown that reproduction can occur over a salinity range of 15 to 45‰ (Moreira and Yamashita 1975). *Euterpina acutifrons* is an important link in the marine trophic web serving as food source for both adult and larval fishes (Pouchet and de Guerne 1887; Lebour 1918; Blin 1923; Carvalho 1945; Marques 1951; Thayer et al. 1974).

In an earlier paper, Moreira (1975) reported that salinity tolerances for Brazilian populations of *E. acutifrons* from Santos were very different from those of populations of this species from São Sebastião. This in itself is not surprising since the salinity regimes of the two areas are different. The salinity in the Santos Estuary varies widely from 17 to 30‰ depending on the tide and season of the year, while in São Sebastião Channel the salinity is approximately 35‰ throughout the year. Water temperatures in both areas are essentially the same, ranging from 19° to 30°C depending upon season. It was not determined, however, if the observed differences in salinity tolerances of the two populations were genetically or environmentally induced. Subsequently, a study was initiated to resolve this question by measuring metabolic response patterns of specimens from both populations to different thermal-salinity regimes. It soon became apparent that environmental parameters other than temperature and salinity were factors in determining the metabolic response patterns of these copepods.

A detailed chemical analysis of the water in Santos Bay is not available, but great numbers of tankers and other vessels continuously operate near shore, discharging ballast water and contaminating seawater and adjacent regions with petroleum. In addition, there are a large number of industries that discharge wastes directly into the water. One sample analysis of Santos Bay seawater was found to contain 270 ppb lead and 200 ppb nickel (unpublished data). Furthermore, to minimize the effects of human waste or degradation products, approximately 400 tons of chlorine are added monthly near shore. The data presented in this paper demonstrate that

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metabolic response patterns of *E. acutifrons* to the normal fluctuations found in estuarine systems were significantly altered by the water quality of Santos Bay water.

MATERIALS AND METHODS

The copepods were collected in two fixed locations off the coast of the State of São Paulo, one in Santos Bay (lat. 23°59'S; long. 46°19'W), the other in São Sebastião Channel (lat. 23°50'S; long. 45°25'S). Collections were made with a nylon plankton net (20 mμ) during the winter when water temperatures averaged approximately 21°C. All samples were brought immediately into the laboratory whereupon *E. acutifrons* were sorted from the plankton using a mouth pipette under a binocular microscope. The copepods were placed in 2-l crystallizing dishes, 20 cm in diameter and 15 cm high. In the first two series of experiments, the copepods were placed in the water obtained from the collection points, i.e., copepods from São Sebastião Channel were placed in São Sebastião water (35‰) and copepods from Santos were placed in Santos water (28‰). In the last two series of experiments, copepods from São Sebastião were placed either in Santos water or in São Sebastião water diluted to 28‰. The copepods were maintained under temperature and photoperiod regimes approximating field conditions: 19°-24°C and 11 L:13 D. The copepods were fed with *Phaedactylum* and *Platymonas* daily and kept in the laboratory at least 1 wk before being used in the respiration experiments.

Oxygen uptake was determined using Cartesian diver respirometers (Holter 1941), which have a total volume of 8-13 μl. Only nongravid females were used. Two or three copepods were placed in each diver, depending upon the salinity/temperature regime of the experiment. The oxygen uptake was determined during a 2-h interval. The first 30-min reading was discarded; after this initial reading, uptake rates remained constant.

Oxygen uptake rates were measured under the following environmental conditions: São Sebastião animals maintained in São Sebastião water, Santos animals in Santos water, and São Sebastião animals in Santos water, 15°, 20°, 25°, 30°, and 32°C at 15, 25, 35, 45, and 55‰ salinities. The oxygen uptake of São Sebastião animals maintained in São Sebastião water diluted to 28‰ was determined at 15°, 25°, and 30°C over the same salinity ranges used in the other experiments. Ten determinations were made under each set of environmental conditions. Distilled water or freeze-concentrated brine was added to filtered seawater to attain the desired salinities. Salinities were determined by titrating against silver nitrate (Harvey 1955).

Dry weights for the copepods were obtained using a Torbal[3] torsion balance, 0.01 mg sensitivity. The copepods were rinsed with distilled water and dried at 70°C for 24 h before they were weighed. Three replicates of 200 nongravid females from each area of collection were used. Results were expressed as microliters of oxygen per milligram per hour. Significant difference of means was calculated by the method of Simpson et al. (1960) for small samples.

The metabolic data obtained in the first three series of experiments were analyzed statistically using multiple regression techniques. The basic experimental design used in this study is usually referred as a factorial design. Specifically, the plan was a 5 × 5 factorial using five levels of temperature and five levels of salinity, making in all 25 combinations of experimental conditions. Since 10 determinations of oxygen uptake were made in each combination, a total of 250 observations were made in each series. Thus, the 250 observations may reasonably be considered as continuous responses of a function of the two factors and interactions.

Oxygen uptake data were analyzed as percentage of oxygen consumption relative to that at 25°C and 35‰ salinity for São Sebastião animals in São Sebastião water and at 25°C and 25‰ salinity for Santos animals in Santos water and São Sebastião animals in Santos water, i.e., the rate under these "standard" conditions was assumed to be 100%, and rates obtained under other regimes were calculated as the percent deviation from that rate. Since the observations are treated as percentage measurements generated by data from binomial populations, the transformation $Y = \text{arc sin } \sqrt{x}$, where x is observed percent respiration, is appropriate to stabilize variances (Mendenhall 1968). Analysis of variance for this data indicated which of the factors (temperature, salinity, or temperature-salinity interactions) had significant effects on the metabolism of the copepods. The program was run on an IBM 360 computer.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Animals From São Sebastião in São Sebastião Water (35‰)

The metabolic rate of *Euterpina acutifrons* from São Sebastião which were maintained in water from São Sebastião Channel was less influenced by changes in salinity than were the other groups of *E. acutifrons* (Figure 1). Rate did, however, increase with increasing temperature up to 30°C; at 32°C, rates either leveled off or decreased. Greatest increases in respiration rates were observed between 15° and 20°C. These increases are reflected in the relatively high metabolic rates within this thermal range obtained from this group of animals.

At 20°C metabolic rates were not significantly different over the entire salinity range of 15-55‰, and at 15°C the copepods were able to regulate their metabolism over a range of 25-55‰. At higher temperatures (25°, 30°, and 32°C) rates generally were lower at the salinity extremes (15, 45,55‰) and highest at 35‰. Rates varied from a minimum of 4.87 to a maximum of 22.36 μl/mg h^{-1} dry weight (Figure 1).

Statistical analysis indicated that 66% of the observed variability in the rates could be explained by the temperature-salinity combinations (Table 1), although the linear effect of temperature was the single significant factor (1% level). The linear effect of salinity, the quadratic effects of the temperature and salinity, and the temperature-salinity interaction did not contribute significantly to the observed changes in respiration rates. Figure 2A shows the response surface contours fitted over the experimental design.

TABLE 1.—Analysis of variance of data for *Euterpina acutifrons* (São Sebastião animals in São Sebastião water, 35‰). T = temperature, S = salinity.

Variable	r^2	Significance level
T	0.54953	1%
T^2	0.65769	Not significant
S	0.65796	Not significant
S^2	0.65885	Not significant
T × S	0.65933	Not significant

Animals From Santos in Santos Water (28‰)

In the Santos animals maintained in Santos water, the rate of oxygen uptake also increased over the temperature range to 30°C for the entire salinity range. In most of the salinities, the largest metabolic increase occurred between 25° and 30°C. This contrasts with São Sebastião copepods which exhibited the largest increase between 15° and 20°C. The Santos animals did not show the metabolic regulation observed in the São Sebastião animals maintained in São Sebastião water, and tended to have low metabolic rates at the salinity extremes, i.e., 15, 45, and 55‰. Highest rates occurred at salinities of 25-35‰. The rates varied from a minimum of 7.97 to a maximum of 28.20 μl/mg h^{-1} dry weight (Figure 1).

Statistical analysis indicated that only 46% of the observed variability in the respiration rates of these animals could be explained by the temperature-salinity combinations (Table 2). The significant factors were the quadratic effects of temperature and salinity (0.05% level) and the linear effect of salinity (0.05% level). The temperature-salinity interaction was not a significant factor. Figure 2B shows the response surface contours fitted over the experimental design.

TABLE 2.—Analysis of variance of data for *Euterpina acutifrons* (Santos animals in Santos water 28‰). T = temperature, S = salinity.

Variable	r^2	Significance level
T^2	0.24350	0.05%
S^2	0.28955	0.05%
S	0.46193	0.05%
T × S	0.46198	Not significant

Animals From São Sebastião in Santos Water

Transfer of São Sebastião copepods into water from Santos markedly altered their metabolic responses, especially their response to salinity. Respiration rates increased with temperature up to 25°C at the extreme salinities (15, 45, 55‰) and up to 30°C at salinities of 25 and 35‰, before leveling off or decreasing. The copepods which were transferred to Santos water did not regulate metabolically at any temperature at the salinity extremes. Lowest rates were obtained at salinities of 15 and 55‰, and the highest rates were observed at 25‰ at 15° and 25°C. At 30° and 32°C, peak metabolic rates occurred at 35‰ (Figure 1). Rates varied from a minimum of 6.80 to a maximum of 37.23 μl/mg h^{-1} dry weight (Figure 1).

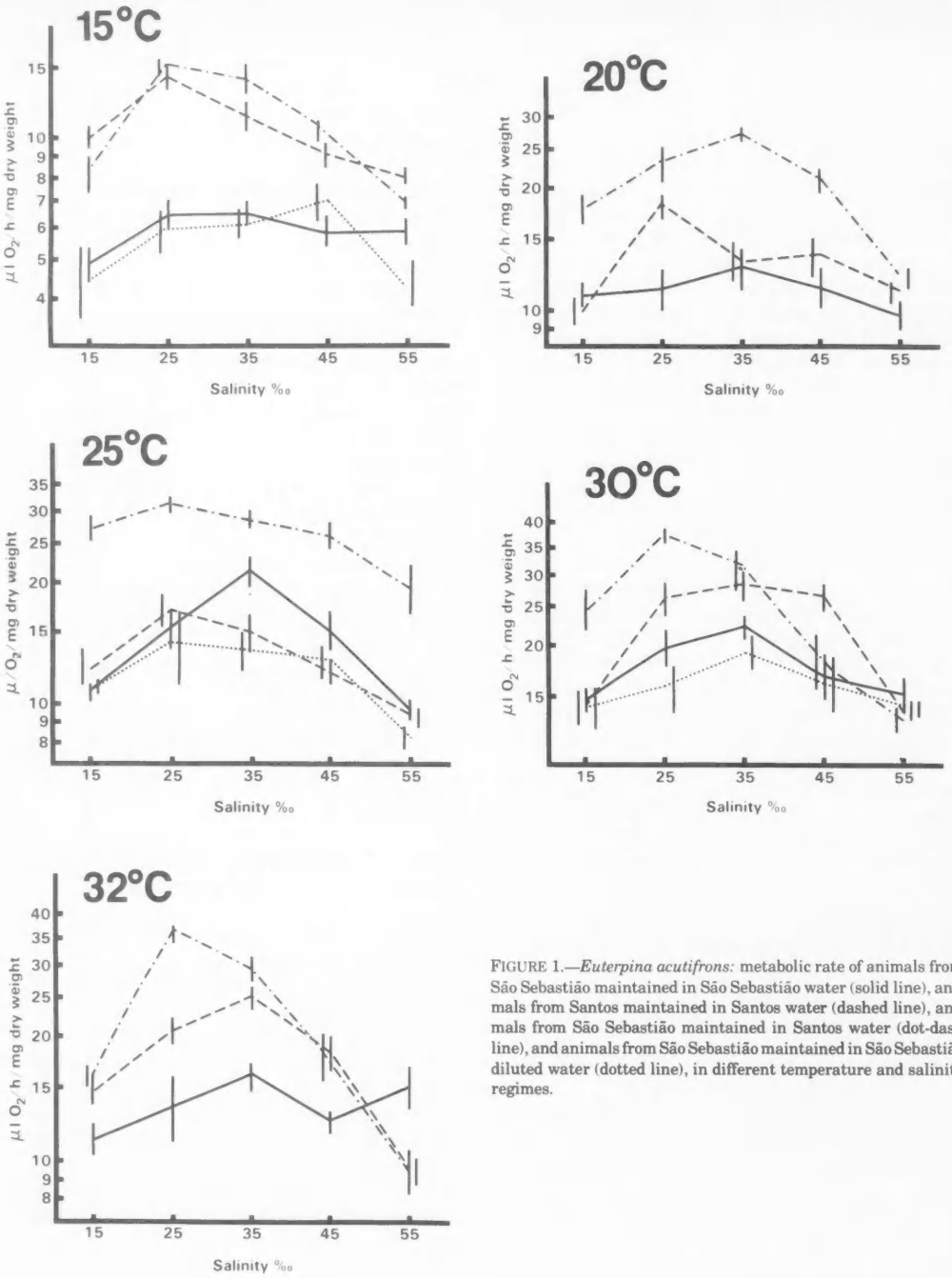

FIGURE 1.—*Euterpina acutifrons:* metabolic rate of animals from São Sebastião maintained in São Sebastião water (solid line), animals from Santos maintained in Santos water (dashed line), animals from São Sebastião maintained in Santos water (dot-dash line), and animals from São Sebastião maintained in São Sebastião diluted water (dotted line), in different temperature and salinity regimes.

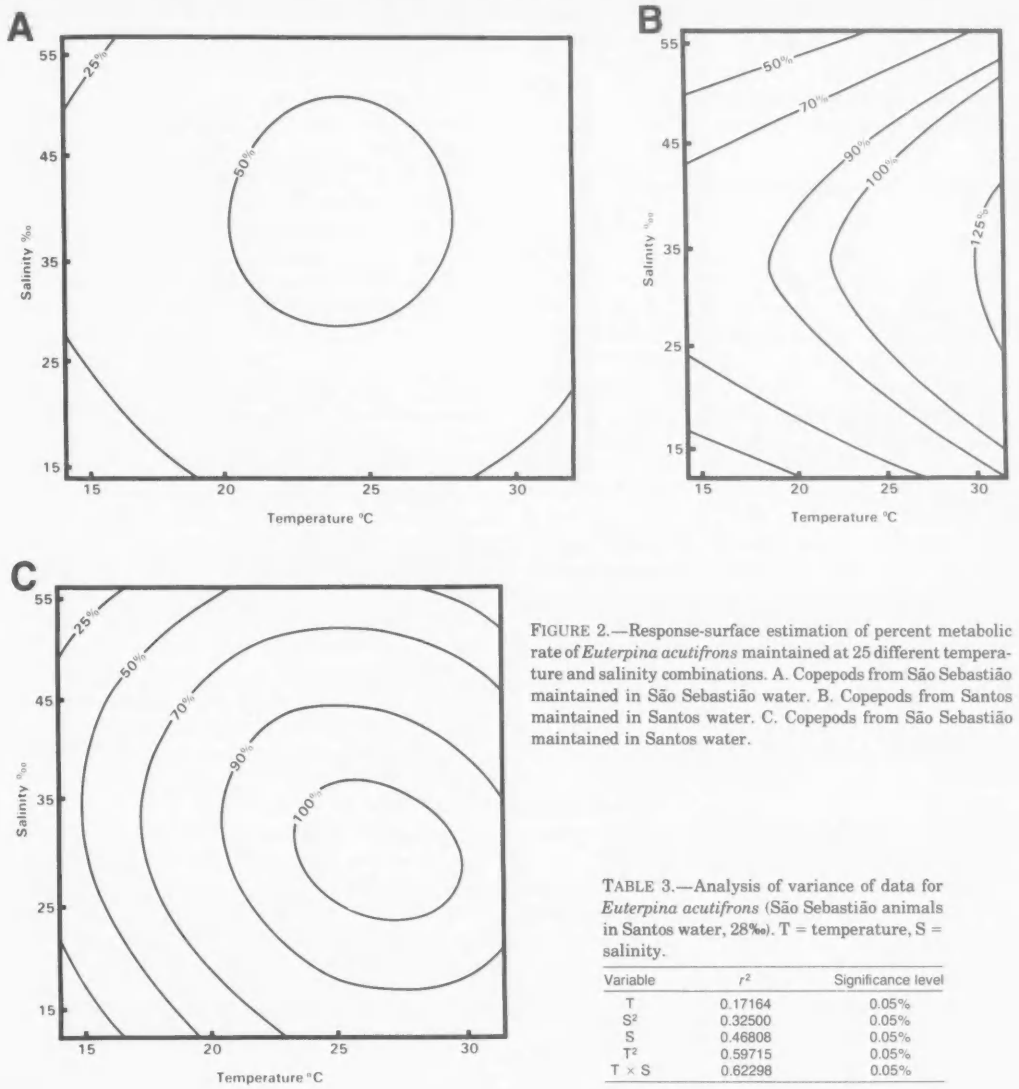

FIGURE 2.—Response-surface estimation of percent metabolic rate of *Euterpina acutifrons* maintained at 25 different temperature and salinity combinations. A. Copepods from São Sebastião maintained in São Sebastião water. B. Copepods from Santos maintained in Santos water. C. Copepods from São Sebastião maintained in Santos water.

TABLE 3.—Analysis of variance of data for *Euterpina acutifrons* (São Sebastião animals in Santos water, 28‰). T = temperature, S = salinity.

Variable	r^2	Significance level
T	0.17164	0.05%
S^2	0.32500	0.05%
S	0.46808	0.05%
T^2	0.59715	0.05%
T × S	0.62298	0.05%

All of the analyzed factors, i.e., linear temperature and salinity, as well as the quadratic effect of these factors, and the temperature-salinity interaction, contributed significantly (0.05% level) to the observed variability in respiration rates (Table 3). A total of 62% of the variability could be explained by these various factors. Figure 2C shows the response surface contours fitted over the experimental design.

Animals From São Sebastião in São Sebastião Diluted Water

In this series the respiration experiments were run at three temperatures to test whether or not the results obtained for Santos animals were the result of acclimation to a lower salinity. The respiration rates at 28‰ were essentially the same as those for animals maintained in undiluted São

Sebastião water. At 15°, 25°, and 30°C, metabolic rates were not significantly different over the range of 15-45‰. The rates varied from a minimum of 4.32 to a maximum of 19.17 μl/mg h^{-1} dry weight (Figure 1).

DISCUSSION

In Brazilian waters, populations of *E. acutifrons* thrive over a wide range of salinities and variable salinity alone does not seem to be a limiting factor in their distributional patterns (Tundisi 1972; Moreira and Yamashita 1975). Indeed, of the various environmental variables tested, temperature alone significantly affected the metabolic rates of these copepods. The present data demonstrate that specimens of copepods from the unpolluted São Sebastião Channel have the capability of metabolic regulation over a wide range of salinities when tested using São Sebastião water. On the other hand, marked diminution in the capability to regulate metabolically at salinity extremes was noted in *E. acutifrons* from the Santos population and specimens from São Sebastião maintained in Santos water. For both groups of animals salinity, as well as temperature, proved to exert a statistically significant effect at the 5% level (or less) on their oxygen uptake rates. These marked changes in metabolic control in the copepods taken from or exposed to Santos water compared with that of copepods from São Sebastião are depicted in Figure 2.

While we did not measure population densities of the *E. acutifrons* in our two study areas (Santos Bay and São Sebastião Channel), there is some indication in the literature that population size is sensitive to polluted waters. Gabriel et al. (1975) reported a decrease in abundance of this species in the Milford Haven Estuary following its development into the largest oil port in the United Kingdom in the 1960's, and there are several examples that indicate that pollutants can affect the survival of copepods and planktonic larvae. Barnes and Stanbury (1948) have studied the toxic action of copper and mercury salts on the copepod *Nitocra spinipes* and verified that mercuric chloride is a very effective poison; in contrast, these animals are very resistant to copper. D'Agostino and Finney (1974) have found that copper and cadmium inhibit growth and development of the copepod *Tigriopus japonicus* at 0.064 mg/l and 0.044 mg/l, respectively. Heinle (1969) suggested that the high mortality rate of *Acartia tonsa* in a power plant effluent was due to the chlorination of the cooling water, correlating the apparent periodicity in the mortality rate with the chlorination schedule. Latimer et al. (1975) studied the toxicity of 30-min exposures of residual chlorine to two species of copepods, *Limnocalanus macrurus* and *Cyclops bicuspidatus thomasi*. The predicted "safe" concentrations were 0.9 mg/l for *L. macrurus* and 0.5 mg/l for *C. b. thomasi*. Roberts et al. (1975) studied the acute toxicity of chlorine to some estuarine species, including molluscan larvae, copepods, shrimps, and fishes. They found that molluscan larvae and *Acartia tonsa* were the most sensitive species tested, with 48-h TL_{50} values at chlorine levels <0.005 ppm. Gray (1974) demonstrated that lead ($Pb(NO_3)_2$) at 0.3 ppm reduced the growth rate of the marine ciliate protozoan *Cristigera* by 11.7% and at 0.15 ppm by 8.46%. Mercury was found to have an effect on survival, metabolism, and behavior of the planktonic larvae of *Uca pugilator* (DeCoursey and Vernberg 1972; Vernberg et al. 1973). Generally, larvae are much more sensitive to toxicants than are adults and very low concentrations of a toxicant can interact with environmental factors to cause increased mortalities among larvae (Vernberg 1975).

Detailed chemical analyses of Santos water obviously are needed, but the very high concentration of lead and nickel which were found in one sample, plus the oil and other industrial effluents that are being discharged, leave little doubt that the Santos Estuary is highly polluted. Data presented in this paper strongly suggest that specimens living in the Santos Estuary do so at a high cost energetically. This high metabolic cost for survival following exposure to salinity extremes would almost certainly be a factor limiting the distribution of *E. acutifrons* in polluted estuaries, since fluctuating salinity regimes are characteristic of this environment. Results obtained in this study highlight the fact that the physiological responses of marine organisms may be markedly modified if test animals are taken from or exposed to polluted waters.

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DESCRIPTION OF LARVAE OF A HIPPOLYTID SHRIMP, *LEBBEUS GROENLANDICUS*, REARED IN SITU IN KACHEMAK BAY, ALASKA

EVAN HAYNES[1]

ABSTRACT

Larvae of *Lebbeus groenlandicus*, a hippolytid shrimp, were reared in situ in Kachemak Bay, Alaska, from the first zoea (Stage I) through the megalopa (Stage III). Each of the three stages is described and illustrated, and then compared with descriptions of larvae of *Lebbeus* spp. given by other authors.

Information on the larval stages of the genus *Lebbeus* is meager. Pike and Williamson (1961), in their summary of the generic characteristics of *Spirontocaris* and related genera, note that the only larva of *Lebbeus* known for certain is a larva of *L. polaris* dissected from a well-developed egg. During studies on rearing larvae of pandalid shrimp for descriptive purposes (Haynes 1976, 1978), I succeeded in rearing larvae of *L. groenlandicus* to the megalopa stage. This report describes and illustrates each of the two zoeal stages and megalopa of *L. groenlandicus*, and compares the stages obtained from rearing in situ and from plankton in Kachemak Bay with provisionally identified larvae of *L. groenlandicus* reported by other authors.

METHODS

A complete discussion of rearing technique, methods of measurement, techniques of illustration, and nomenclature of gills and appendages is given by Haynes (1976). Briefly, the rearing technique consists of obtaining Stage I zoeae from known parentage in the laboratory and then rearing the zoeae to postlarvae in 500-ml flasks suspended upright beneath the surface of the sea. Cast skins and larvae removed from the flasks were examined in the laboratory to determine sequence and morphology of each stage. Larval stage was also verified using larvae from plankton reared in the same manner as larvae obtained in the laboratory.

In the illustrations (Figures 1-3), for clarity, setules on setae are usually omitted but spinulose setae are shown. The terms are defined as follows:

setose - set with bristles (setae)
spinose - bearing many spines
spinous - spinelike
spinulose - set with little spines.

The figures are in part schematic and represent typical setal counts.

STAGE I ZOEA

Total length of Stage I (Figure 1A) 6.9 mm (range 6.4-7.4 mm; 10 specimens). Live specimens characterized by bright orange color extending along ventral surface of body from antennules to fourth abdominal segment, orange gut, small orange chromatophore at anus, and greenish internal thoracic organs; remainder of zoea translucent. Rostrum slightly sinuate, without teeth, about two-thirds length of carapace. Carapace with dorsal rounded prominence at base of rostrum and near posterior edge; no supraorbital spines. Usually at least two minute spinules occur along ventral margin of carapace immediately posterior to pterygostomian spine.

ANTENNULE (FIGURE 1B).—First antenna, or antennule, consists of an unsegmented cylindrical basal portion and two distal conical projections; largest conical projection bears four aesthetascs of various lengths; smallest conical projection bears a single heavily plumose seta.

ANTENNA (FIGURE 1C).—Consists of inner flagellum (endopodite) and outer antennal scale (exopodite). Flagellum two-segmented, about twice length of scale; distal segment styliform and terminating in narrow projection. Two simple

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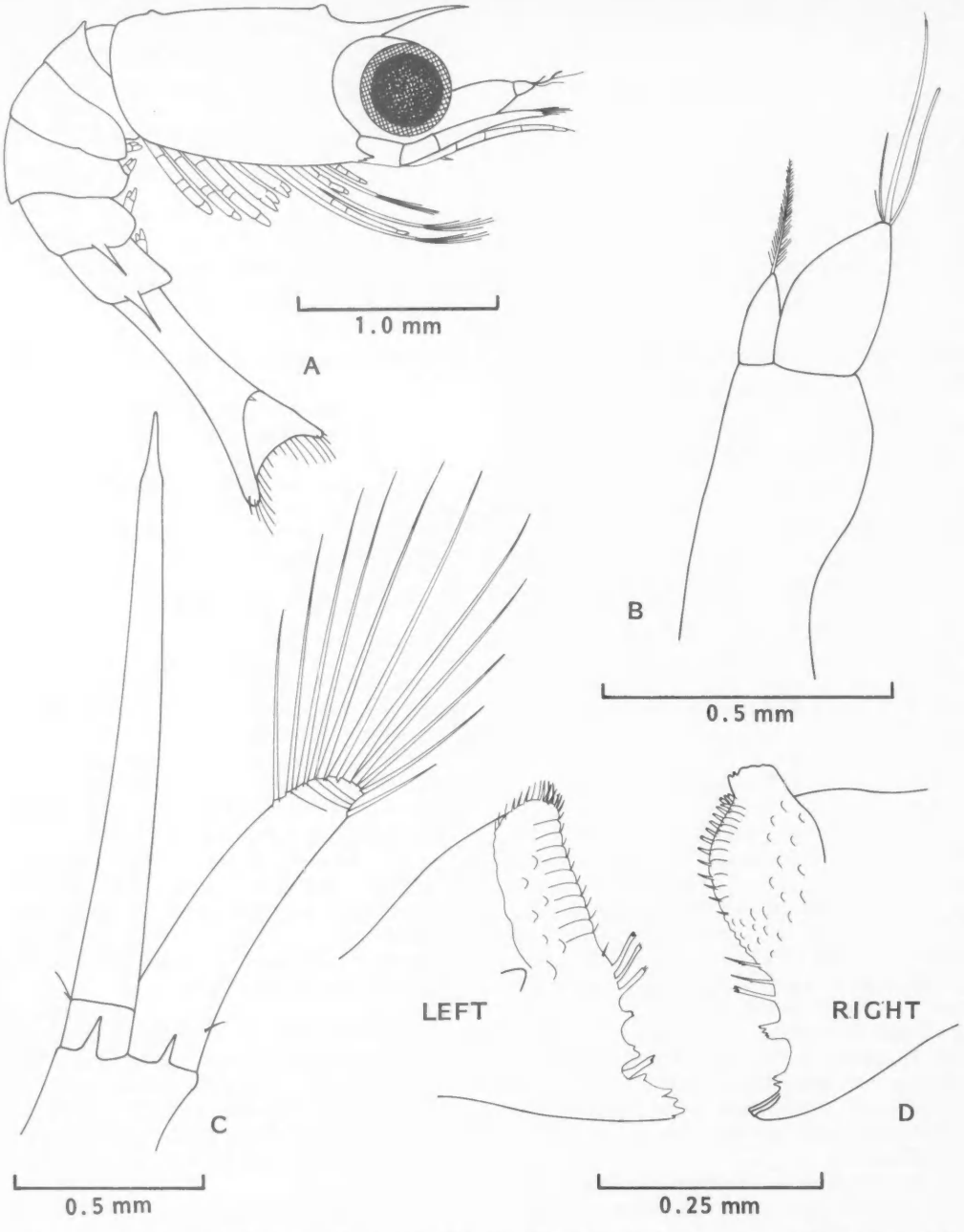

FIGURE 1.—Stage I zoea of *Lebbeus groenlandicus*: A, whole animal; B, antennule; C, antenna; D, mandibles (right and left).

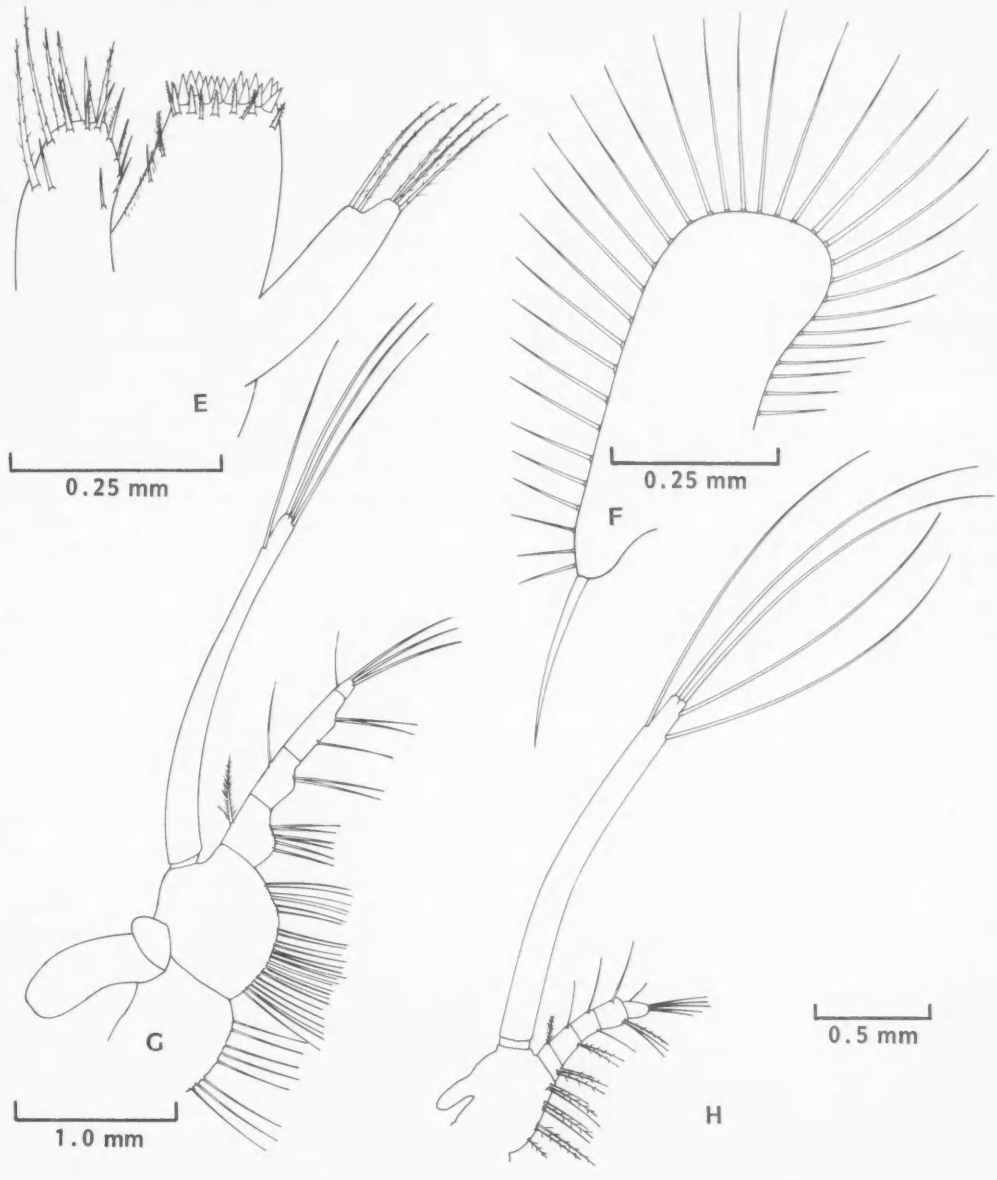

FIGURE 1.—Stage I zoea of *Lebbeus groenlandicus*: E, maxillule; F, scaphognathite of maxilla; G, first maxilliped; H, second maxilliped.

setae occur at joint. Antennal scale distally divided into four segments (proximal joint often incomplete) and fringed with 11 heavily plumose setae along terminal and inner margins. A small seta often occurs proximally near lateral margin. Protopodite bears two simple spines ventrally, one at base of flagellum and one at base of scale.

MANDIBLES (FIGURE 1D).—Without palps;

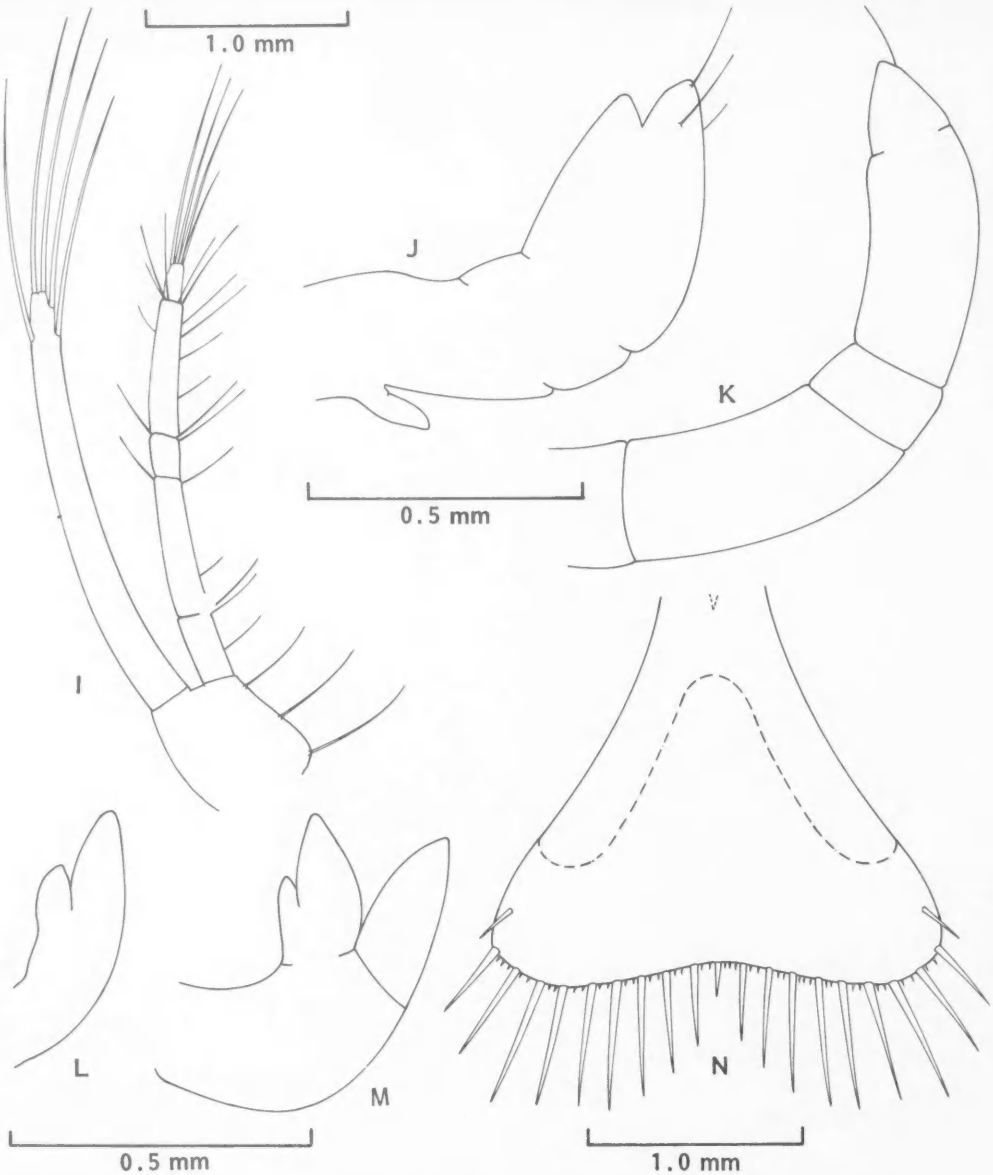

FIGURE 1.—Stage I zoea of *Lebbeus groenlandicus:* I, third maxilliped; J, first pereopod; K, third pereopod, L, first pleopod; M, second pleopod; N, telson.

well developed. Incisor process of left mandible bears five teeth, one of them located near movable premolar denticle (lacinia mobilis), in contrast to triserrate incisor process of right mandible. Both mandibles bear well-developed denticles along terminal margin. Truncated end of molar process of right mandible formed into curved lip. Only left mandible bears a subterminal process.

MAXILLULE (FIGURE 1E).—First maxilla, or maxillule, bears coxal and basial endites and an endopodite. Proximal lobe (coxopodite) bears 15 setae, most of them spinulose. Median lobe (basipodite) bears 24 spines terminally, 9 of them spinulose; and 2 spines subterminally, 1 of them plumose and the other simple. A series of fine hairs occurs in vicinity of the simple spine. Endopodite originates from lateral margin of basipodite and bears three terminal and two subterminal spinulose setae. No evidence of outer seta on maxillule.

MAXILLA (FIGURE 1F).—Bears platelike exopodite (scaphognathite) with 33 long, plumose setae along outer margin, and a longer, thick seta at the proximal end. Endopodite not segmented; setae spinous, setation formula 2, 2, 1, 2, 3. Both basipodite and coxopodite bilobed. Basipodite bears 29 setae, 14 on distal lobe and 15 on proximal lobe. Coxopodite bears 23 setae, 5 on distal lobe and 18 on proximal lobe.

FIRST MAXILLIPED (FIGURE 1G).—Protopodite segmented; bears 27 setae on distal segment and 8 on proximal segment, most of them spinulose. Endopodite four-segmented; setation formula 4, 3, 3, 7. Basal segment of endopodite bears conspicuous setulose spine. Exopodite segmented at base; bears four natatory setae. Epipodite distinctly bilobed.

SECOND MAXILLIPED (FIGURE 1H).—Protopodite not segmented; bears nine setae, five of them spinulose. Endopodite five-segmented; fourth segment expanded somewhat laterally; terminal segment tipped by five setae and bears single seta subterminally; basal segment bears conspicuous setulose spine like that on basal segment of endopodite of first maxilliped; setation formula 6, 4, 2, 3, 4. Exopodite about three times longer than endopodite; bears five natatory setae. Epipodite present but not bilobed.

THIRD MAXILLIPED (FIGURE 1I).—Protopodite not segmented; bears three setae. Endopodite five-segmented; as long as exopodite; number of setae somewhat variable. Exopodite bears five natatory setae. No epipodite.

FIRST PEREOPOD (FIGURE 1J).—Endopodite relatively short, wide, and partially segmented; chela partially formed; dactylopodite bears three simple spines. Exopodite a small lobe.

SECOND PEREOPOD.—Similar in shape to first pereopod except narrower, exopodite smaller, and chela more deeply cleft.

THIRD (FIGURE 1K) TO FIFTH PEREOPODS.—Each pair essentially identical except that they decrease slightly in size from third to fifth. No exopodites.

PLEOPODS.—First pleopod (Figure 1L) slightly cleft, without joints or setae. Second pleopod (Figure 1M) bilobed; outer lamella segmented; inner lamella usually only partially segmented but bears bud of appendix interna. Third to fifth pleopods essentially identical to second pleopod except both lamellae distinctly segmented.

ABDOMEN AND TELSON (FIGURES 1A, 1N).—Abdomen consists of five segments and telson (somite six is fused with telson in Stage I). Fourth and fifth abdominal segments each with pair of posterolateral spines nearly as long as segments themselves. Telson slightly emarginated distally; bears 19-21 densely plumose setae; small spinules occur between bases of all setae except two outermost pairs. Enclosed uropods visible. Anal spine present.

STAGE II ZOEA

Total length of Stage II 8.3 mm (range 8.1-8.7 mm; 8 specimens). Color similar to Stage I zoea but more diffuse. Rostrum (Figure 2A) arched upward; slightly blunter than in Stage I; without teeth. Carapace bears supraorbital, antennal, and pterygostomian spines in addition to several spinules along anteroventral margin.

ANTENNULE (FIGURE 2B).—Shows considerable change from Stage I. Largest conical projection segmented at tip; terminal segment bears three setae of different lengths; proximal segment bears six groups of five aesthetascs each in addition to row of four aesthetascs laterally and single seta distally. Smallest conical projection bears three nonplumose setae, one long and two short. Peduncle of antennule rounded laterally, not segmented, and bears five plumose setae that originate ventrally.

ANTENNA (FIGURE 2C).—Flagellum of antenna still two-segmented, but slightly stouter and projection at tip smaller than in Stage I; a few

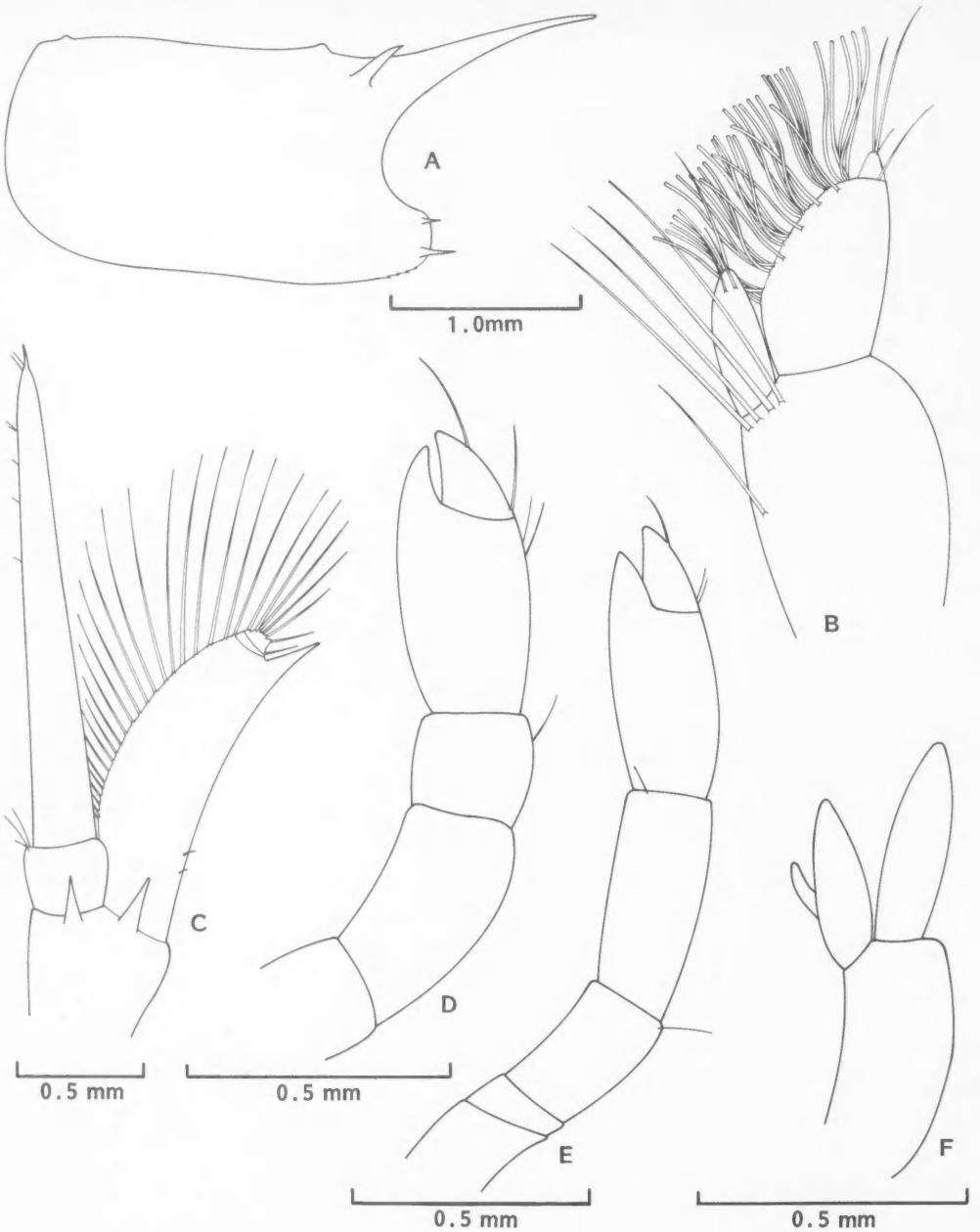

FIGURE 2.—Stage II zoea of *Lebbeus groenlandicus*: A, carapace; B, antennule; C, antenna; D, first pereopod; E, second pereopod; F, second pleopod.

small setae occur along lateral margin. Antennal scale distally divided into two segments and fringed with 29 or 30 thin, plumose setae along terminal and inner margins; distal outer projection a stout spine. Protopodite bears two stout spines, one at base of flagellum and other at base of scale.

MANDIBLES, MAXILLULE, AND MAXILLA.—Essentially identical to Stage I except scaphognathite of maxilla usually bears 35 setae along outer margin, in addition to the longer and thicker seta at proximal end, and proximal cleft slightly deeper.

MAXILLIPEDS.—Essentially identical to Stage I except exopodites of first, second, and third maxillipeds bear 5, 16, and 16 natatory setae, respectively.

FIRST PEREOPOD (FIGURE 2D).—Segmented; without exopodite; chela functional.

SECOND PEREOPOD (FIGURE 2E).—Adult in shape; chela functional; ischiopodite articulates somewhat laterally with basipodite. No exopodite.

THIRD TO FIFTH PEREOPODS.—Similar to Stage I except ischiopodite articulates somewhat laterally with meropodite and basipodite.

PLEOPODS.—First pleopod slightly more developed than in Stage I but still only about one-third length of second pleopod and without appendix interna. Second pleopod (Figure 2F) larger and narrower than in Stage I; outer lamella about one-fourth longer than inner lamella; both lamellae and appendix interna fully segmented at their bases. Third to fifth pleopods essentially identical to second pleopods.

ABDOMEN AND TELSON.—Posterolateral spines on fourth and fifth abdominal somites still present, those on fourth somite being only slightly shorter in relation to length of somite than in Stage I. Telson essentially identical to Stage I except segmented from sixth abdominal segment and bears 20 or 21 densely plumose setae. Uropods still enclosed.

STAGE III (MEGALOPA)

Total length of Stage III 7.5 mm (range 7.4-7.6 mm; two specimens). Antennal spine of carapace larger and pterygostomian spine smaller than in Stage II; no evidence of minute spinules along anteroventral margin. Rostrum (Figure 3A) short; bears single tooth at base in addition to dorsal protuberance. Antennules similar in shape to adult; outer flagellum six-segmented; inner flagellum five-segmented; peduncle three-segmented,

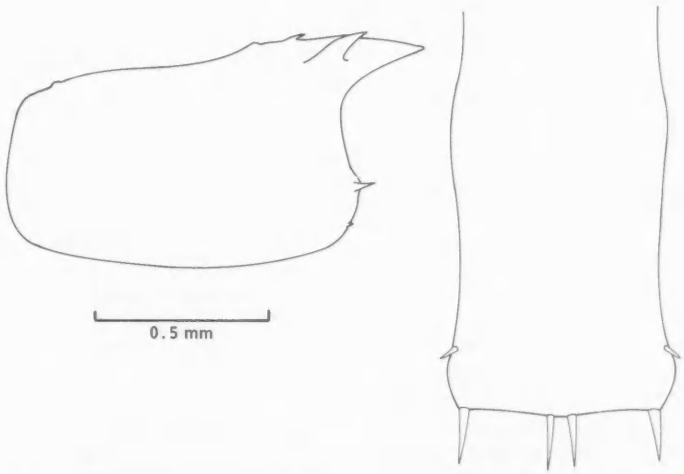

FIGURE 3.—Stage III (megalopa) of *Lebbeus groenlandicus*: A, carapace; B, telson.

lateral spine of proximal segment well developed. Antennal flagellum with at least 30 segments; about four times length of scale. Mandibles with unsegmented palps bearing four or five short teeth. Endopodite of maxillule reduced. Maxillipeds shaped as in adult, exopodites reduced. Dactylopodites of first and second pereopods well developed; carpopodite of second pereopod six- (sometimes seven-) segmented. Lateral margins of pleopods fringed with setae; appendix internae with minute cincinnuli. Posterolateral spines on abdominal segments four and five remnant or lacking. Telson (Figure 3B) rectangular in shape; bears two pairs of spines terminally and one pair laterally (one or two additional spines may occur centrally on terminal margin). Uropods exposed; fully developed except transverse hinge not complete.

COMPARISON OF LARVAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

Under the name "*Spirontocaris*-larva No. 1A," Stephensen (1935) included four specimens that were morphologically identical to zoeae provisionally identified by him as Stage I *S. polaris* (= *Lebbeus polaris* (Sabine)) except that they differed by lacking spines on abdominal segments four and five, exopodites on any pereopods, or free uropods. He regarded these four zoeae as belonging to either *Spirontocaris groenlandica* (= *L. groenlandicus*), *S. gaimardii* (= *Eualus gaimardii* (H. Milne Edwards)), or *S. spinus* (Sowerby). Pike and Williamson (1961) have shown that the absence of spines on abdominal segments four and five eliminates the zoeae from being either *E. gaimardii* or *S. spinus*. They agree with Stephensen that his specimens of "*Spirontocaris*-larva No. 1A" are closely allied to zoeae he tentatively described earlier (Stephensen 1917, 1935) as *S. polaris* (= *L. polaris*). They suggest, therefore, that Stephensen's "*Spirontocaris*-larva No. 1A" probably belongs to the genus *Lebbeus* and specifically to *L. groenlandicus*.

Comparison of my zoeae of *L. groenlandicus* with the descriptions given by Stephensen for "*Spirontocaris*-larva No. 1A" shows that "*Spirontocaris*-larva No. 1A" are not zoeae of *L. groenlandicus*. My Stage I zoeae bear remnant exopodites on the first and second pereopods and lateral spines on abdominal segments four and five, but Stephensen's Stage I zoeae bear neither the exopodites nor the spines. My Stage I zoeae do not bear supraorbital spines, the peduncle of the antennule is without joints or a ventral spine, and there is no indication of the carpopodite of the second pereopod being jointed; Stephensen's Stage I zoeae bear supraorbital spines, the peduncle of the antennule is three-jointed and bears a distinct ventral spine, and the carpopodite of the second pereopod is partially jointed. In addition, the chelae of the first and second pereopods are not as well formed in my Stage I zoeae as they are in Stephensen's Stage I zoeae.

Several of the morphological characteristics described by Stephensen as pertaining to "*Spirontocaris*-larva No. 1A" are typical of later stage zoeae, a fact already noted by Pike and Williamson (1961) in their discussion of the morphology of the zoeae of *L. polaris* and which prompted them to suggest that Stephensen's zoeae were actually in the second, or penultimate, zoeal stage. Even if Stephensen was mistaken in identifying his zoeae as Stage I rather than Stage II, the morphological differences between my zoeae and his are too great to consider them identical species. My Stage II zoeae bear spines on abdominal somites four and five and the telson is segmented from the sixth abdominal somite, whereas Stephensen's zoeae do not bear spines on abdominal somites four and five and the telson is not segmented from the sixth abdominal somite. Also, in my Stage II zoeae the peduncle of the antennule does not bear a ventral spine and is unsegmented but in Stephensen's zoeae the peduncle bears a ventral spine and is segmented.

I have no further evidence on the identity of Stephensen's "*Spirontocaris*-larva No. 1A." Of the three members of the genus recorded from Greenland waters, *L. polaris, L. groenlandicus,* and *L. microceros* (cf. Holthuis 1947; Squires 1966), *L. microceros* was not recorded by Stephensen. Apparently it is rare and its larvae have not been described. Also, the advanced development of Stephensen's "*Spirontocaris*-larva No. 1A" makes it unlikely that it belongs to another genus of the spirontocarid group (cf. Pike and Williamson 1961). Apparently Stephensen's "*Spirontocaris*-larva No. 1A" is either the zoea of *L. microceros* or that of another species of *Lebbeus* not yet recorded from Greenland waters.

On the basis of descriptions of "*Spirontocaris*-larva No. 1A" by Stephensen (1935) and a late stage embryo of *Hippolyte polaris* (= *L. polaris*) by Krøyer (1842), Pike and Williamson (1961)

characterized larvae of the genus *Lebbeus* as having two (or three) zoeal stages, five-segmented pereopods, and a small rostrum in Stage I, and pereopods without exopodites in the last zoeal stage. My description of larvae of *L. groenlandicus* confirms the generic characteristics for *Lebbeus* larvae as given by Pike and Williamson. As noted by Pike and Williamson, however, larvae are described for only a few species of hippolytids, including the genus *Lebbeus*, and further confirmation of the generic characteristics of the larvae is desirable.

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PREDICTING ABUNDANCE OF STRIPED BASS, *MORONE SAXATILIS*, IN NEW YORK WATERS FROM MODAL LENGTHS[1]

HERBERT M. AUSTIN[2] AND CLARENCE R. HICKEY, JR.[3]

ABSTRACT

The abundance of cohorts for any given year class of striped bass, *Morone saxatilis*, prior to their leaving Chesapeake Bay is inversely related to the modal length of fish in that year class 2 yr later in New York waters. The modal length of bass in their third year migrating into the New York area is a reliable index of the abundance of that year class. When back extrapolated modal lengths at the end of the second year of life are considered for the dominant year classes in the New York fishery (ages III-VI), a high degree of inverse correlation is found between age II and modal length and reported landings suggesting that this is an effective method of predicting the abundance of the stock for the fishery.

In discussing natural fluctuations in fish populations, Royce (1972) posed the question, " . . . can we forecast their occurrence to take maximum advantage of periods of high abundance and protect populations during periods of scarcity?" This question is pertinent to the striped bass, *Morone saxatilis*, stocks of the Atlantic coast of the United States. The Atlantic coast commercial catch of this species, while following a pattern of fluctuations, has been in an upward trend in recent years, apparently as a result of an increasing abundance of fish (Koo 1970; McHugh 1972). This increasing abundance has been reflected by an increased commercial harvest in the State of New York. Concurrently, although not as well documented, is an increase in the number of recreational fishermen utilizing the resource. Both phenomena necessitate the gathering of management information while the resource is still in good condition.

Most (>80%) of the New York commercial harvest of striped bass occurs in the waters of eastern Suffolk County (Figure 1) where the major fisheries are primarily with haul seine and pound net. Fish taken in this region are predominantly of Chesapeake Bay origin (Neville et al. 1939; Alperin 1966; Schaefer 1968, 1972; Koo 1970; Austin and Custer 1977; Austin and Hickey;[4] Texas Instruments, Inc.[5]).

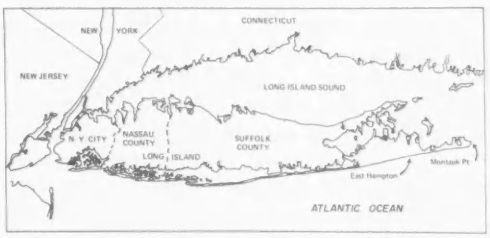

FIGURE 1.—Location of Long Island, N.Y., and the southeastern tip near Montauk Point where striped bass were collected during 1972 and 1974.

This study was designed as one phase of a program to tag and monitor "short" or prerecruit striped bass (less than the legal, 406-mm New York State limit). As stated by Talbot (1966), little is known of these fish outside of their nursery areas. Monitoring of these fish, then, permits study of the next year's catch, a segment of the striped bass population often overlooked in fishery investigations.

Prerecruit striped bass in New York waters of eastern Long Island are predominantly 2- and

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[4]Austin, H. M., and C. R. Hickey, Jr. 1974. Migration and mortality of striped bass tagged in eastern Long Island, p. 11-16. Proc. Am. Littoral Soc./N.Y. Ocean Sci. Lab. Fish Tag Seminar, Dec. 1974, Montauk, N.Y.

[5]Texas Instruments, Inc. 1976. Report on relative contribution of Hudson River striped bass to the Atlantic coastal fishery. Unpubl. rep., 110 p. Texas Instruments, Inc., Dallas, Tex.

3-yr-old fish which are making their first annual migration from their Chesapeake Bay nursery areas to the northern summer feeding ground (Austin and Hickey see footnote 4). The concentrated study of one age-group of fish permits monitoring of the cohorts for successive years starting with first departure from their home grounds and, thereby, permits a description of differences or variations in migration and abundance on an annual basis, as well as an accurate evaluation of year class mortality in successive years.

METHODS AND MATERIALS

Prerecruit striped bass were randomly removed from the catches of commercial haul seine and pound net fishermen in the waters of East Hampton on the southeastern end of Long Island, N.Y. (Figure 1). Samples were collected during May and June 1972 and April-June 1974, thus the age II fish were of the 1970 and 1972 year classes, respectively. Fork lengths were measured in the field to the nearest millimeter and scale samples were removed for age determination. The fish were then tagged (Floy[6] FD-69B anchor tags) and released. The initial purpose of the study was tagging of prerecruit fish to monitor the seasonal migration and mortality of cohorts as they reached legal size in the different states. The feasibility study was focused on the 1970 and 1972 year classes. Large differences in the modal size of the fish in their third year (II+) existed between the two year classes (Figure 2). The smaller sized 1970 year class of fish were from the most abundant Chesapeake Bay year class on record (Schaefer 1972). Examination of the literature shows that the length of cohorts may be inversely proportional to the abundance or density of the fish (Stevens 1977; Texas Instruments[7]), suggesting to us that the length of the striped bass, when they first appear in New York waters, could be an indicator of year class strength and subsequently a means of predicting stock abundance in local waters. Consequently the focus of the study was redirected towards examination of these differences.

Schafer (1968, 1972) stated that most commercially harvested striped bass in New York are of four age-classes, III-VI. Based on this, Schaefer

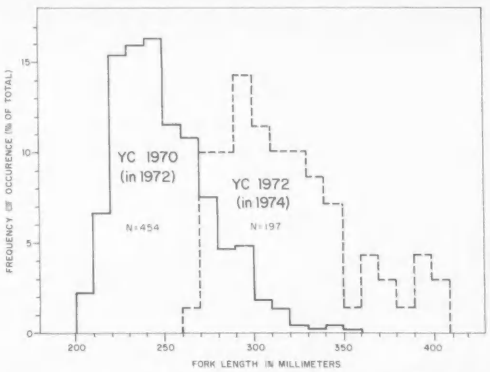

FIGURE 2.—Length-frequency distribution of age II striped bass captured by commercial fishing gear near eastern Long Island, N.Y., during 1972 and 1974.

(1972) related the New York harvest to a 4-yr mean brood production (year class strength; expressed as annual mean number of juveniles per standard seine haul in Chesapeake Bay, Md.) 3 to 6 yr prior to the harvest. He concluded that approximately 70% of the variability in annual New York landings could be explained by annual fluctuations in year class strength in Maryland waters of Chesapeake Bay.

We hypothesized that the growth rate of striped bass, and, therefore, the body length at the end of the 2-yr residence time in the Chesapeake Bay nursery grounds, is a density dependent function with the length inversely proportional to the year class abundance (number of fish). This hypothesis was tested via a correlation analysis using modal lengths at age II+ (our data combined with published data of Alperin 1966 and Schaefer 1968) and year class abundance indices supplied by the Maryland Department of Natural Resources. The analyses were performed using a Hewlett-Packard Model 9100B programmable calculator with an X-Y plotter, which provided both a regression line and a correlation analysis and coefficient.

The relationship resulting from the above analysis suggested that the density dependent hypothesis is true. Since Schaefer (1972) described a relationship between the annual New York harvest (reported commercial landings) of striped bass and the Chesapeake Bay year class abundance, and since we have described a probable relationship between year class abundance and modal length at age II+ in New York waters, it seemed reasonable to test the correlation between

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[7]Texas Instruments, Inc. 1975. First annual report for the multiplant impact study of the Hudson River estuary. Unpubl. rep., vol. 1, p. VIII-8-VIII-12. Texas Instruments, Inc., Dallas, Tex.

the New York harvest and the modal length at age II+ via Model II correlation analysis.

These analyses were performed in an effort to describe a method for predicting the commercial harvest (and therefore the apparent abundance) of striped bass in New York waters. As each of the several steps in the analyses were dependent on the results of those previously calculated, they are discussed in more detail along with the results below.

The reliability of the suggested technique for predicting the abundance of striped bass in New York waters is dependent on several assumptions:

1) The Chesapeake Bay stock of fish is the major contributor of striped bass to the New York commercial fishery, as suggested by the several authors noted above;
2) The annual relative contribution of the several Atlantic coastal breeding stocks to the coastal stock of fish and, therefore, to the New York fishery remains constant or that it fluctuates or cycles in a consistent manner;
3) The commercial fishery for striped bass in New York effectively collects representative "samples" of the Chesapeake Bay stock of fish; this assumption appears to be valid based upon the relationships described by Schaefer (1972), Texas Instruments, Inc. (see footnote 5) and those described herein, and based upon our observations and those of Schaefer (1972) that many size classes of fish are present in the commercial catch—small age II prerecruits to large mature fish >16 kg total weight;
4) The forecast of commercial striped bass landings is based upon past historical landings in relation to past life history events of the species (year class abundance and length at age II+) and does not reflect changes in commercial fishing effort or any changes in the contributions to the reported landings by recreational fishermen; we have assumed a constant fishing effort, as did Schaefer (1972), and thus compared our results with his; while we recognize the weakness in this assumption, there is no alternative as there is no estimate of effort.

RESULTS AND DISCUSSION

Year Class Strength and Modal Size

The lengths of striped bass at age II+ near Long Island are probably related to ecological circumstances encountered by the fish during their first 2 yr of residence in the rivers of Chesapeake Bay (density, competition, amount of available food). Similarly, Cushing (1968) found a close relationship between the mean length of age III Atlantic herring, *Clupea harengus*, and the density of their food source in the sea, and Clark (1967) described reduced growth rates for sunfish, *Lepomis*, due to overcrowding, excessive competition, and reduced food supply. It has also been demonstrated by Anthony (1971) that the growth of young (age I and II) Atlantic herring is inversely related to their abundance, and Wagner (1969) has stated that in most fishes the growth rate per individual is inversely related to their density.

If an inverse relationship exists between the abundance of a year class of striped bass and the cohort length at age II+, a similar relationship should exist between the commercial harvest (as an index of abundance) and the length at age II+, assuming that fishing effort remains approximately constant. To test this hypothesis, age II+ modal length data for year classes 1970 and 1972 (Figure 2) were combined with other published modal length data for year classes at age II+ in New York waters from Alperin (1966) and Schaefer (1968) (Table 1), providing a total of eight annual data points. A correlation analysis was performed between these eight annual modal lengths of age II+ fish and their respective Chesapeake Bay year class strengths 2 yr earlier (Figure 3). The year class strength data (supplied by the Maryland Department of Natural Resources) are expressed as the annual mean

TABLE 1.—Comparison of observed and computed modal fork lengths for age II striped bass in New York waters.

Year class	Year class strength[1]	Observed modal length at age II (mm)	Computed modal length at age II[2] (mm)
1954	5.2	[3]313	318
1958	18.1	[4]285	278
1959	1.3	[3]335	330
1960	6.4	[3]310	314
1961	14.4	[3]290	289
1962	12.2	[3]300	296
1970	26.8	[5]245	251
1972	8.5	[5]295	307
Mean		297.9 ±53.0	297.9 ±50.4
Standard deviation		26.5	25.2
$t_r = 6.99$			
$n = 8$			
$P<0.001$			

[1]Courtesy Joseph Boone, Maryland Department of Natural Resources, Annapolis, Md., data expressed as annual mean number of age 0+ juveniles per standard seine haul.
[2]Based on the relationship $Y = 333 - 3X$, where Y is the modal length of age II+ fish and X is the strength of the year class (Figure 3).
[3]Extrapolated from Schaefer (1968).
[4]Extrapolated from Alperin (1966).
[5]Data from the present investigation.

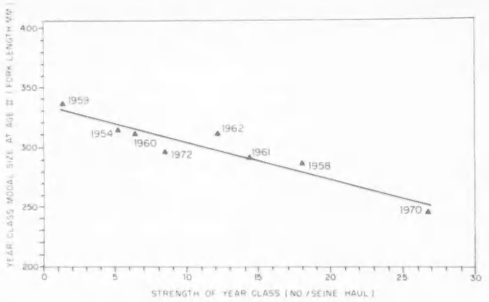

FIGURE 3.—Modal size (mm fork length) of age II striped bass from Long Island waters as a function of Chesapeake Bay year class strength. Year classes are indicated.

number of age 0+ juveniles per standard seine haul near the Maryland shores of Chesapeake Bay. These are the same data used by Schaefer (1972). The relationship ($Y = 333 - 3X$) yielded a correlation coefficient of -0.95 ($r^2 = 0.90$), suggesting that 90% of the annual variation in modal length at age II+ for striped bass in New York waters can be explained by annual fluctuations in year class abundance in the waters of Chesapeake Bay.

Modal Size and the New York Commercial Harvest

The equation described above ($Y = 333 - 3X$) was used to calculate (and thus to estimate) modal lengths of age II+ fish for those 8 yr for which actual modal lengths exist. A t-test comparison between the observed age II modal sizes and those computed using the correlation formula above showed no significant difference at the 0.001 probability level (Table 1). Since no significant difference existed between the observed and calculated modal lengths, the assumption was made that reliable modal lengths could be calculated for years in which no actual measurements exist. The equation described above was, therefore, used to estimate modal lengths of age II+ striped bass for all years between 1954 and 1972, using the corresponding year class abundance data. A correlation analysis was then performed (similar to that done by Schaefer 1972) between the New York landings of striped bass (Y) and a 4-yr mean of the computed modal lengths of age II+ fish 1 to 4 yr prior to harvest (X). The relationship ($Y = 15{,}205{,}309 - 46{,}859X$) (Figure 4A) yielded a correlation coefficient of -0.86 ($r^2 = 0.74$) significant at the 0.001 probability level ($t_r = 6.06$, $n = 13$). This expression permits the hindcasting of New York landings as well as a forecast 1 yr in advance, with 95% confidence limits. The hindcasts and 1-yr forecasts (for 1975) are superimposed on the actual New York landings in Figure 5A.

As stated by Schaefer (1968, 1972), the New York harvest is predominantly fish of ages III-VI. Close examination of his catch data for 1962, however, revealed that age VII fish, although <2% of the catch in number, could constitute a significant proportion of the catch by weight. Schaefer's (1968) age-frequency distribution shows that in 1962 the age III fish outnumbered the age VII by about 10:1. Using the mean age-weight relationships of Mansueti (1961) as 1.8 lb at age III and 12.5 lb at age VII, the age III fish in Schaefer's (1968) 1962 catch thus outweighed the age VII fish by less than 1.5:1. Similarly, the age VI fish (mean

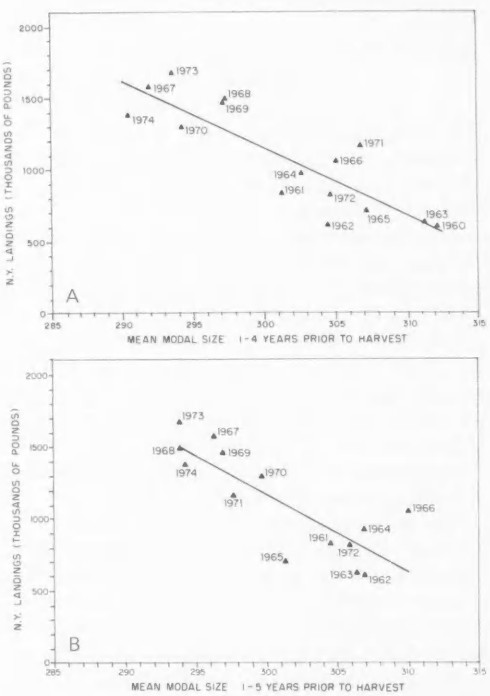

FIGURE 4.—Relationship of New York commercial landings of striped bass to the mean modal size at age II: A) 1 to 4 yr prior to harvest; B) 1 to 5 yr prior to harvest.

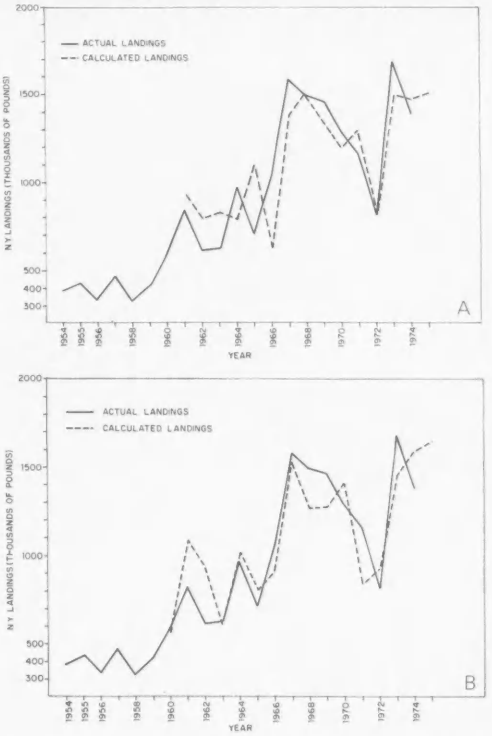

FIGURE 5.—Actual New York commercial landings of striped bass from 1954 through 1974 with calculated landings through 1975 superimposed using: A) 4-yr mean modal sizes of age II fish; B) 5-yr mean modal sizes of age II fish.

weight 8.1 lb) outnumbered the age VII fish by 2:1, but outweighed them by only 1.3:1.

It was apparent that during some years the New York harvest of striped bass may be dominated by five age-groups rather than four, as suggested by Schaefer (1972). Another correlation analysis was, therefore, performed between the New York landings (Y) and a 5-yr mean of the computed modal sizes of age II+ fish 1 to 5 yr prior to harvest (X). This 5-yr function was expressed as a linear relationship ($Y = 17{,}315{,}491 - 53{,}810X$) (Figure 4B) with a correlation coefficient of -0.83 ($r^2 = 0.69$), significant at the 0.001 probability level ($t_r = 5.05$, $n = 12$). Although this coefficient was reduced slightly from that of the 4-yr function above ($r = -0.86$), the fit of estimated-to-actual landings (with 95% confidence limits) was better for many years (Figure 5B) and was closer to the actual landings than the calculated predictions of Schaefer (1972) (Table 2).

Size, Age, and Migration

As stated, age II+ modal sizes may be computed. Another method of size determination at age II+ is by back calculation of scale radii from larger, older fish. Although no age II modal sizes determined by this method were used in the predictive models, our attempts to do so produced some interesting information. Mansueti (1961) described the body length-scale length relationship of striped bass as an allometric linear function, permitting the back calculation of size at each year of age using the scale radii method. Scales from 142 age III striped bass captured in eastern Long Island waters during 1973 (year class 1970) were made available to the authors by the New York State Department of Environmental Conservation. The ages were rechecked and the fork lengths at age II determined by back calculation from body length:scale radii ratios. The length-frequency distribution of back-calculated data was bimodal, with equal peaks at 205 mm and 235 mm. The second peak was 4.1% lower than the observed unimodal size of 245 mm. Although the back calculated values were slightly lower than the observed, the fit suggests that back calculations may be used for obtaining age II sizes of striped bass during years when these data are lacking.

Unpublished length-frequency data for age II striped bass of the year classes 1968, 1969, and 1971 taken in the Virginia rivers of the Chesapeake Bay System were made available to the authors by John V. Merriner of the Virginia Institute of Marine Science. These data showed bimodal distributions similar to that of the back-calculated age II lengths above (Merriner pers. commun.). Merriner suggested that multimodal frequencies occurred because the fish were from different river systems. Merriner's data were from Virginia rivers while our data (Austin and Hickey

TABLE 2.—Comparison of actual and calculated commercial landings of striped bass in the State of New York 1972-75.

Year	Actual landings[1]	Calculated landings 4-yr function[2]	Calculated landings 5-yr function[2]	Calculated landings by Schaefer (1972)
1972	818,150	926,903	852,860	908,000
1973	1,673,984	1,447,975	1,496,965	1,455,000
1974	1,378,529	1,592,301	1,477,594	1,607,000
1975	1,137,074	1,639,160	1,500,732	—

[1]Courtesy Fred Blossom, National Marine Fisheries Service, NOAA, Patchogue, N.Y.
[2]Forecasts using the linear regression formulae discussed in the text.

see footnote 4) suggest that the bass we examined for back calculation of length were from both Maryland and Virginia rivers, which could explain the differences in the results of the back calculations and the observed lengths. These data suggest that the size-frequency distribution of age II striped bass on Long Island could be bimodal rather than unimodal. The fact that they were not may be due to striped bass migrating by size rather than by age. Two observations of prerecruit striped bass near Long Island lend support to this theory: 1) 100% of the small 454 sublegal fish tagged in 1972 were age-group II, and 2) only 28% of the 696 sublegal fish tagged in 1974 were age-group II (year class 1972), the remaining 72% were age-groups III (65%) and IV (7%). Those fish probably were the larger 1972 and the smaller 1971 and 1970 fish. This large overlap in length ranges permitted an intermingling of the age-classes during the migration of 1974.

Management Implications

The size increments between different year classes at the same age, and the size differences of individuals within the same year class have several implications:

1) Faster growing large individuals of any given year class or a less abundant year class of larger individuals are subject to earlier exploitation in Chesapeake Bay and along the entire Atlantic seaboard;
2) Slower growing individuals or small individuals of a large year class may be recruited several months later than normal in Chesapeake Bay, but perhaps not until a full year later among the northern Atlantic States; a late recruitment in the Chesapeake area might result in more available fish to the fisheries in the other coastal states when the fish migrate out of the bay;
3) Projecting sizes of fish on the basis of age or vice versa may be invalid, e.g., age II fish in 1972 compared with age II fish of Merriman (1941) or Mansueti (1961).

The use of a mean 4- or 5-yr modal function for prediction of landings treats all year classes equally. A weighted mean providing greater representation to more abundant year classes might result in more accurate predictions of landings. Such a method could be used by any State simply by monitoring the spring catches of age II+ prerecruit fish taken by commercial fishermen. This would require, in New York for example, annual monitoring of the spring run with measurements of sublegal fish. The use of observed modes rather than computed modes for prediction of landings will probably result in more accurate estimates, as suggested in Table 3.

TABLE 3.—Comparison of actual New York commercial landings of striped bass with those calculated using computed and observed age II modal values, for years in which sufficient empirical data exist.[1]

Item	1964	1965
Actual N.Y. landings	925,500	702,935
4-yr function:		
Landings calculated using:		
Computed modes	1,021,090	807,881
Empirical modes	913,314	618,102
5-yr function:		
Landings calculated using:		
Computed modes	799,588	1,098,771
Empirical modes	—	849,631

[1]Computed and observed age II modal values are those on Table 1.

The eastern New York commercial harvest of striped bass is primarily dependent upon the year class abundance of the Chesapeake Bay stock. The harvest is influenced not only by the larger and older individuals, but also by the annual recruitment of age III fish, especially when dominant year classes are present.

Knowledge of Chesapeake Bay year class strength or age II+ modal sizes in New York waters offers a means of forecasting the New York commercial harvest, and thus the apparent abundance of striped bass in New York waters.

If, as suggested, the level of the New York harvest is primarily related to the Chesapeake Bay stock of fish, than the former can be used as a qualitative measure of the latter.

Such predictive tools as those discussed should be flexible to allow for the occurrence of more than four age-groups of fish in the catch. This may be especially important when dominant year classes are present for several years. Necessary, then, is the annual monitoring of the prerecruit fish in the commercial catch by age or year class, length, and weight. Age-weight data are especially important as commercial landings are recorded by weight of catch and not by numbers of fish. Differences noted between calculated and observed landings may be due to environmental variability, changes in fishing effort, the dominance of a particular year class in the fishery, and the fluctuation in the relative contributions of fish from the several At-

lantic coastal breeding grounds. Future research and managment efforts should take these into consideration.

ACKNOWLEDGMENTS

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OBSERVATIONS ON A WHITE-SIDED DOLPHIN, *LAGENORHYNCHUS ACUTUS*, PROBABLY KILLED IN GILL NETS IN THE GULF OF MAINE

On 20 July 1976, a white-sided dolphin, *Lagenorhynchus acutus*, was observed floating with its beak out of the water on Jeffreys Ledge, Maine (lat. 43°09'N, long. 70°04'W). The 201-cm long female weighed 113.2 kg and was freshly dead, still bleeding freely from symmetrical injuries to the left and right sides of both the upper and lower jaws and the flippers. The lungs contained foamy materials and were mottled white, indicating drowning as the immediate cause of death. Many gill nets were present in the area, and the symmetrical nature of the injuries indicated that the animal had become entangled in the mesh, drowned, and perhaps been freed or discarded during hauling of the net. A humpback whale, *Megaptera novaengliae*, was entangled in a gill net for 2 h before freeing itself on the same day in the same general area.

Gross autopsy revealed several cysts in the abdominal muscles of the lower left side and a 5 cm × 7.5 cm yellow, pussy abscess 15 cm anterior and dorsal to the right mammary gland, perhaps caused by a bladderworm stage (plerocercoid) of *Monorygma grimaldi* (Geraci et al.[1]). No other parasites were found, although all major organs except the brain were inspected. Tissue and organ weights are shown in Table 1. The length and weight of this animal fit well on a regression line developed for this species (Geraci et al. see footnote 1). From a length-age relationship (Geraci et al. see footnote 1), it is likely that this female was between 2½ and 3 yr old, and was immature.

The stomach contained 980 g of food, including four 25- to 30-cm herring, *Clupea harengus*, three partly digested (total weight 340 g) and one skeleton (15 g); and one partly digested short-finned squid, *Illex illecebrocus* (anterior mantle length 17.5 cm, weight 90 g), with remains of 10 other squid of this species (represented by 5 complete pairs of beaks plus 5 single anterior beaks). Mean length of anterior beaks (± SD) was 1.42 ± 0.03 cm, corresponding to mantle lengths from 17 to 19 cm (Testaverde[2]). Also 10 left and 11 right otoliths from silver hake, *Merluccius bilinearis*, (mean size ± SD = 1.15 ± 0.06 cm) indicated consumption of at least 11 fish of 22-26 cm fork length (Nichy 1969).

From these data and the literature it appears that *C. harengus* and *I. illecebrocus* are staples in the summer diet of white-sided dolphins. A 161-kg female collected on 14 September 1954, off Cape Cod contained 12 fresh herring, digested fish (apparently herring), and squid (Schevill 1956). A 180-cm long male driven ashore with pothead whales, *Globicephala melaena*, in Newfoundland on 30 July 1954, contained herring and short-finned squid (Sergeant and Fisher 1957). Short-finned squid was the most common food in the stomachs of white-sided dolphins which mass-stranded at Lingley Cove, Maine, on 6 September 1974; however, no herring were found despite the fact that "brit" herring were present in the cove (Geraci et al. see footnote 1). Smelt, *Osmerus mordax*, remains, were found in five individuals; silver hake had been eaten by one individual; and unidentified crustacean remains were found in another stomach.

Schools of white-sided dolphins were unusually common in the Gulf of Maine in 1976, perhaps because squid were abundant, possibly as a result of this year's unusually high sea temperatures

TABLE 1.—Tissue and organ weights of a *Lagenorhynchus acutus* from Jeffreys Ledge, Maine. Weights not corrected for blood loss.

Tissue or organ	Weight (kg)	Tissue or organ	Weight (kg)
Muscle	69.0	Left kidney	0.473
Blubber and fins	24.5	Right adrenal	0.011
Gastrointestinal tract	6.8	Left adrenal	0.010
Liver	3.2	Spleen	0.084
Heart	0.959	Right ovary	0.0051
Right lung	1.117	Left ovary	0.0047
Left lung	1.149	Bones[1]	5.4
Right kidney	0.476	Total	113.2

[1]Bones were bleached and dried in the laboratory.

[1]Geraci, G., S. A. Testaverde, D. J. St. Aubin, and T. H. Loop. 1976. A mass stranding of the Atlantic white-sided dolphin, *Lagenorhynchus acutus:* a study into pathobiology and life history. Unpubl. manuscr., 166 p. submitted to Marine Mammal Commission by New England Aquarium, Boston.

[2]Testaverde, S.A. 1975. An informal discussion concerning the cestode *Phyllobothrium* sp. in squid, *Illex illecebrocus illecebrocus* and its possible relationship to marine mammals. Unpubl. manuscr., 20 p.

(Anonymous 1976; Prescott and Moore 1976). Silver hake, normally of variable abundance here (Bigelow and Schroeder 1953) was also abundant during 1976. On several different occasions, groups of 6-30 white-sided dolphins were seen by one of us (SKK) swimming close to pods of either finback whale, *Balaenoptera physalus,* or humpback whale, *Megaptera novaeangliae,* and apparently feeding with them.

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RECIPROCAL HYBRIDIZATION BETWEEN THE CALIFORNIA AND GULF OF CALIFORNIA GRUNIONS, *LEURESTHES TENUIS* AND *LEURESTHES SARDINA* (ATHERINIDAE)

The California grunion, *Leuresthes tenuis,* and the Gulf of California grunion, *L. sardina,* are the only fishes that temporarily leave the water during spring high tides to deposit their eggs in beach sand (Walker 1952). The eggs develop in the nearly dry sand and hatch when uncovered and agitated by the surf of the next series of high tides.

The grunions have an allopatric distribution. The California grunion ranges from Monterey Bay, Calif., to Bahia Magdalena, Baja California Sur. The Gulf grunion is endemic to the Gulf of California, ranging from Bahía Concepción, Baja California Sur, and Guaymas, Sonora, Mexico to the mouth of the Río Colorado (Moffatt and Thomson 1975).

Recent comparisons show that morphological, physiological, and behavioral differences exist between the grunions. Morphologically very similar, the most diagnostic characterictics distinguishing them are lateral scale row counts; the mean number in *L. tenuis* is 75 and in *L. sardina* is 55. Gulf grunion adults are also significantly longer, more slender, have a smaller eye diameter, and are more lightly pigmented than those of the California grunion (Moffatt 1974; Moffatt and Thomson 1975). Gulf of California grunion have wider embryonic and larval thermal tolerances, a higher larval preferred temperature, and wider larval salinity tolerances (Reynolds and Thomson 1974a, b, c; Reynolds et al. 1976, 1977; Moffatt 1977).

Light response remains positive in Gulf grunion through adulthood, whereas the response shifts from positive in the larvae to negative in the adults of the California grunion (Walker 1952; Reynolds and Thomson 1974c; Reynolds et al. 1977). In response to the shorter wave period in the northern Gulf of California, the duration of the spawning act of the Gulf grunion females is much briefer than that of the California grunion females (Thomson and Muench 1976; Muench 1977).

Only recently has the congeneric status of the grunions been recognized (Moffatt 1974; Moffatt and Thomson 1975). Evidence to date indicates that the California grunion, the less primitive of the two species, has adapted to the less fluctuating tidal and thermal regimes of the California coast, following isolation from an ancestral type by the

Baja California peninsula (Moffatt and Thomson 1975; Moffatt 1977).

Hybridization and hybrid survival experiments have been widely used as indices of divergence and have made valuable contributions as a tool in the definition of phylogenetic relationships (Hubbs 1967, 1970). In an attempt to further illuminate the relationship between the grunions, we made artificial and reciprocal crosses and we report on the first successful reciprocal hybridization of *Leuresthes tenuis* and *L. sardina*.

Materials and Methods

Adult grunions, although easily obtained in large numbers, are difficult to maintain and transport alive. On 18 March 1976 (2330 PST), milt from six California grunion males was collected at Scripps Beach, La Jolla Calif., mixed in the beaten yolks of two hen eggs (Bratanov and Dikov 1961), and transported to El Golfo de Santa Clara, Sonora, Mexico. The milt-yolk mixture, maintained between 16° and 20°C, was used to fertilize the eggs from 8 to 10 Gulf grunion females obtained at El Golfo on the following day (19 March) during a spawning run which began about 1700 MST. During this same run Gulf grunion milt was collected from 6 to 7 males, transported in the same manner and used to fertilize California grunion eggs from about 10 females obtained during a run that night at La Jolla at 0115 PST (20 March). One prior and four subsequent attempts to hybridize the grunions were made during the 1975, 1976, and 1977 spawning seasons, but these were unsuccessful because one or both grunions failed to spawn.

The female grunions were rinsed thoroughly in clean seawater before their eggs were stripped directly into the milt-yolk mixture. The mixture was diluted slightly with fresh seawater to increase sperm motility, gently agitated, and kept cool until the end of the spawning run. The eggs were then strained, rinsed with seawater, and placed in plastic refrigerator containers between moist paper towels for transport and incubation.

Conspecific control embryos of each species were obtained by mixing eggs and milt in a bucket of seawater, one-third full, and did not involve the transportation or preservation of milt in hen yolk. When spawning individuals were plentiful, as at the Gulf grunion run on 19 March, six to nine males were stripped per one female in order to achieve maximum fertilization levels (Moffatt 1977).

Both sets of hybrid fertilized eggs and the conspecific controls of *L. tenuis* (18 March) and *L. sardina* (19 March) were transported from San Diego, Calif., to the University of Arizona at Tucson aboard commercial airlines. Upon arrival (22 h postfertilization in *L. sardina* × *L. tenuis* and *L. sardina* controls; 13 h in *L. tenuis* × *L. sardina;* and 32 h in *L. tenuis* controls) each set of eggs was inspected. Their development was monitored daily thereafter.

Both California grunion spawning runs were sparse at La Jolla. Therefore, the greatest portion of eggs and sperm available were devoted to the hybridization experiments and a low conspecific *L. tenuis* sample size resulted. Consequently, the developmental and hatching data reported herein for these embryos are a compilation of these few controls and egg sets obtained on other occasions, incubated at 20°C from 12 h postfertilization (Moffatt 1977).

Yolk-sac larvae of the two hybrids and the conspecific controls were placed in separate tanks containing artificial seawater and raised on newly hatched *Artemia*, freeze-dried marine zooplankton, commercial staple food, and frozen *Artemia* nauplii. Larvae of the hybrids and controls were maintained for nearly 5 mo although initial mortality rates (first 2 mo) in all groups were high (>90%). On 19 August, 141 days posthatching, the aquaria air lines were fouled by compressor oil and the few remaining hybrids and controls died. Only two *L. tenuis* × *L. sardina* and nine *L. sardina* × *L. tenuis* individuals survived to a size (>12 mm) at which the scale rows could be counted. This is not to imply that scales might not have been present prior to this time, merely that no attempt was made to count them.

Results

At 22 h postfertilization, cleavage had progressed to the gastrula stage in *L. sardina* × *L. tenuis* embryos as it had in the *L. sardina* controls. The *L. tenuis* × *L. sardina* hybrids had reached a 32-cell blastodic stage at 13 h postfertilization as do *L. tenuis* embryos.

Artificial fertilization levels in the conspecific controls fell between 85 and 99% during the peaks of their spawning seasons when male to female ratios of 6 or 9:1 were available. The fertilization

levels of both hybrids ranged from 60 to 70%. These diminished levels in the hybrids may have resulted from a combination of several factors such as: the low male to female ratios used (<1:1); decreased sperm motility in the viscous hen-yolk medium; high sperm mortality due to time, starvation, temperature shock, handling, etc. or partial reproductive isolation between the species in the form of mild fertilization block to nonconspecific spermatozoa.

The grunions, *L. tenuis* and *L. sardina*, showed similar developmental rates (Moffatt 1977). Development proceeded normally in the hybrids and at about the same rate as the controls. No unusual embryonic mortality was observed in the hybrids, evidence that these embryos were not gynogenetic hybrids (Moore 1955).

Preliminary trials showed that hen's yolk and seawater alone will not initiate cleavage in Gulf grunion eggs. Precautions were taken to prevent conspecific milt contamination. Preliminary examination of cellular nuclei smears of developing embryos immersed in colchichine revealed somatic chromosome numbers of about 2n = 40 in all four sets of embryos (controls and hybrids), further evidence that these embryos were true diploid hybrids.

Grunion embryos will hatch after vigorous agitation in seawater. On 31 March at 284 h (11.8 days) postfertilization, 65.6% of the *L. sardina* × *L. tenuis* embryos hatched and 66.5% of the *L. tenuis* × *L. sardina* embryos hatched at 272 h (11.4 days). These hatch times are similar to those of the controls. Hatching can be induced in both grunions at 10.2 days postfertilization when embryos are incubated at 20°C (Moffatt 1977).

Newly hatched *L. tenuis* larvae are typically more darkly pigmented; they have a larger eye diameter; they are stronger swimmers; and they are more capable of escaping net capture than newly hatched *L. sardina* larvae (Moffatt 1977). *Leuresthes tenuis* larvae are 10% longer (mean total length = 7.70 mm) than those of *L. sardina* (mean total length = 6.93 mm). The greater length of the California grunion yolk-sac larvae occurs in the postanal region as in the adults. California grunion larvae are also 52% heavier (mean dry weight = 0.340 mg) whereas, the mean dry weight of *L. sardina* equals 0.223 mg (Moffatt 1977). The greater length and weight of the California grunion at hatching may be attributable to the 4.10 times greater ovum volume (Moffatt 1977; Moffatt and Thomson in press).

These differences which distinguish the prolarvae of *L. tenuis* and *L. sardina* were also observed in the hybrids. In most characteristics the *L. tenuis* × *L. sardina* larvae were not visibly distinguishable from the maternal controls (*L. tenuis*), e.g., size, pigmentation, and swimming ability. However, the *L. sardina* × *L. tenuis* larvae appeared to be somewhat intermediate to the controls in extent of pigmentation and swimming ability. At 2 wk after hatching the length and pigment differences between the larvae were more pronounced. Premaxillary teeth were visible in the *L. sardina* × *L. tenuis* larvae but not in the reciprocal hybrids. Again, hybrids closely resembled the maternal controls. Gulf grunion adults typically have much stronger dentition than do the adults of the California grunion (Moffatt and Thomson 1975).

As previously mentioned, the most diagnostic differences between the adult grunions are the lateral scale row counts. Scale counts of the 141-day-old controls were essentially the same as those of the adults (Table 1). The counts of the hybrids were intermediate and significantly different from each other. Those shown by both hybrids were significantly different from those of both parental species. The lateral scale rows of the hybrids were closer in number to those of the maternal controls. Mean counts of *L. sardina* × *L. tenuis* were 32% closer to those of *L. sardina;* and *L. tenuis* × *L. sardina* were 20% closer to *L. tenuis* than to those of the paternal parents, *L. tenuis* and *L. sardina*, respectively.[1] The intermediate counts indicate paternal genome influence and that these are indeed diploid hybrids.

[1]A mean hybrid count greater or less than 65 (the midvalue between the parental species) indicated the affinity to one parent or the other. The numerical affinities (percentages) were calculated as the ratio of the differences between 65 and the hybrid count and between 65 and the adult counts.

TABLE 1.—Means, ranges, *n*, and *P* values of lateral scale row counts observed in 141-day-old hybrids and controls and adults of the grunions, *Leuresthes tenuis* and *L. sardina*.

Parents ♂	♀ *L. tenuis*			♀ *L. sardina*		
	Juveniles	Adults	*P*	Juveniles	Adults	*P*
L. tenuis	$\bar{x}$ = 75.5 (75-76) *n* = 2	$\bar{x}$ = 74.6 (69-80) *n* = 143	>0.6	$\bar{x}$ = 61.8* (61-63) *n* = 9	—	—
L. sardina	$\bar{x}$ = 67.0* (66-68) *n* = 2	—	—	$\bar{x}$ = 55.1 (54-57) *n* = 9	$\bar{x}$ = 55.3 (51-60) *n* = 177	>0.7
	P<0.01	—		*P*<0.001	—	

*Student's *t*-test comparison of the lateral scale row counts between the two hybrids *P*<0.001.

Discussion

Natural hybridizations are reportedly more common among freshwater fishes than among marine fishes (Hubbs 1955). Hubbs (1970) stated that, "teleost hybrids are relatively easily produced and if the parental morphology is similar the hybrids are easily reared." The results of natural and artificial amphibian and teleost crosses have been widely employed for estimating degrees of phylogenetic divergence, revealing systematic patterns, and explaining mechanisms controlling development and differentiation.

Davidson (1968) reports that the closer the phylogenetic relationship between the species hybridized, the less likely the hybrid genome control will be displayed early in development. This is because the mechanical aspects of early development tend to be similar in closely related species and may be primarily under the control of maternal RNA accumulated in the egg prior to fertilization. Davidson believes this, at least in part, accounts for the commonly observed resemblance of hybrids in early developmental stages to the maternal parent. The genetic influence of the paternal genes in the hybrid genome may not be apparent phenotypically until long after the onset of differentiation (Davidson 1968).

It is possible that such mechanisms account for the maternal resemblance pattern observed in the grunion hybrids as well. The hybrids resembled the maternal parents in overall size and body proportions, coloration, swimming ability, net-escape capability, and dentition until long after hatching. Only when the lateral scale rows were counted at 141 days after hatching did the influence of paternal genes become visibly and quantitatively apparent.

The numerous artificial and two natural hybridizations (interspecific and intergeneric) reported among the Atherinidae are reviewed by Hubbs and Drewry (1959), Rubinoff (1961), and Hubbs (1970). Natural hybrids reported between *Menidia menidia* and *M. beryllina* along the Atlantic coast of Florida (Gosline 1948) exhibit intermediate counts (i.e., scales and fin rays). Most of the experimental crosses between these atherinids resulted in low developmental success and low survival rates except those of *M. beryllina* ♀ × *M. menidia* ♂ (Rubinoff 1961). Rubinoff did not report whether any intermediate characteristics existed in these hybrids nor was the reciprocal cross attempted.

Geographically isolated species forms adapt to their respective environments by the evolution of appropriate gene complexes. Then, if sympatry reccurs and hybridization takes place, hybrid individuals will usually be selected against (Mayr 1963; Ford 1964). Hybrids not selected against will usually be successful over only a narrow geographical range, since in animals, natural hybridization is commonly associated with environmental perturbation (Mayr 1963; Manwell and Baker 1970).

The *Menidia* species are sympatric and hybridization does occur in northern Florida, a very narrow portion of the overlap in their ranges (Gosline 1948). Like these species, grunions are marine fishes with similar, but not identical, ecological preferences. However, the grunions are allopatric and natural hybridization is not possible.

According to Mayr (1963), some investigators argue that renewed sympatry with hybridization is required as a process of speciation in order to "perfect isolating mechanisms," and, therefore, unlike the *Menidia* species, the heterospecific status of the grunions may be questioned, especially in light of the hybridization success reported herein. We conclude that, despite our success at hybridizing *L. tenuis* and *L. sardina*, the morphological, physiological, and behavioral distinctions between them warrant their continued recognition as separate species.

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TYCHOPLANKTONIC BLOODWORM, *GLYCERA DIBRANCHIATA*, IN SULLIVAN HARBOR, MAINE

The bloodworm, *Glycera dibranchiata*, is distributed from the Gulf of St. Lawrence to the Gulf of Mexico and from central California to lower California and Mexico. It occurs from intertidal water to 402 m depth (Pettibone 1963), but it is more abundant in shallow coastal water. In Maine and Nova Scotia the worms are dug commercially along the coast from the upper layers of the intertidal sand-silt-clay strata (Dow and Creaser 1970; Anonymous 1974; Glidden[1]).

Spawning bloodworms are briefly pelagic occurring in large numbers as they swarm in the afternoon. Creaser (1973) observed swarming in Maine during June. Simpson (1962) reported swarming both in June and November-December, suggesting a biannual spawning in Maryland. Klawe and Dickie (1957) did not observe swarming by bloodworms in Nova Scotia, although other evidence indicated that the worms spawned in mid-May. They suggested that the worms had a short nocturnal swarming period making them difficult to observe. Simpson (1962) checked this possibility

[1]Glidden, P. E. 1951. Three commercially important polychaete marine worms from Maine: *Nereis (Neanthes) virens, Glycera dibranchiata, Glycera americana*. Rep. to Maine Dep. Sea Shore Fish., Augusta, Maine.

in Maryland by making 40 observations with a night-light between June and November. No worms appeared at the surface under the light.

Individual bloodworms occasionally are pelagic when not spawning. Pettibone (1963), when noting the sightings of others, reported a bloodworm swimming at the surface of Eel pond, Woods Hole, Mass., on the evening of 17 August 1943; another at the surface perhaps at the same pond on 28 January 1876; and another in Delaware Bay on 29 January 1957. No time was given for the two January sightings. On 2 October 1969, E. P. Creaser, Jr. sighted a bloodworm at the surface near a dock on McKown Point, Boothbay Harbor, Maine. The large nonspawner was observed at noon swimming during a flood tide. We have found that nonspawning bloodworms may also occur as fairly abundant members of the tychoplankton—bottom dwellers that are either swept upward with tidal currents or migrate upward at night. This study was originally designed to sample larval Atlantic herring, *Clupea harengus harengus* Linnaeus, and these results will be presented later. The implications of a large incidental catch of bloodworms prompted our writing this note.

Materials and Methods

The site of this investigation, Sullivan Harbor, is an embayment along the eastern coast of Maine. It is divided into northern and southern sectors by a constriction formed by an island, point of land, and ledges (Figure 1). The southern sector opens onto Frenchman Bay, which in turn opens onto the Gulf of Maine. At its upper end, the northern sector constricts into a tidal falls. A narrow channel extends north of the falls eventually bifurcating into broad extensive shallows. Only small streams enter these shallows about 5 km north of the highway bridge. Sullivan Harbor is thus relatively saline (31-32‰).

Six sampling stations were located within the northern sector of the harbor; two in the landward end of the channel (No. 3, 4), two in the seaward end (No. 1, 2), and one at each seaward entrance to the subtidal flats (No. 5, 6). At each station within the channel, four lines of buoyed and anchored nets were set (Graham and Venno 1968). On each line one net fished near the surface and a second at 3 m just above the edge (4 m) of the subtidal channel (Figure 1). A third net fished below the edge at 10 m and a fourth near the bottom (12-20 m). At the entrance to the subtidal flats, one net was suspended near the surface and another at 3 m just above the bottom.

The nets were set at each station at dusk and retrieved at dawn, fishing approximately one tidal cycle. Calibrated meters centered within the nets determined the amount of water strained. The contents of the nets were preserved in the field using a 5% Formalin[2] solution. The sexes of the worms were determined at a later date by inspection of the coelomic contents. Since variable shrinkage of the worms made length measurements unreliable, dry weight was obtained for each worm.

Results

The nets strained 72 bloodworms from tidal currents during 6 of 10 cruises in autumn and winter 1974-75. During 1974, the nets captured 2 worms on 14 October, 7 on 11 November, 2 on 5 December, 51 on 10 December, and 1 on 19 December. During 1975, the nets captured nine worms on 2 December. Only five worms were immature; their weights varied from 0.02 to 0.11 g. Mature females outnumbered mature males about two to one (41:24). The mean weights of the two sexes were similar, 0.57 g, and their range varied from 0.11 to 1.47 g.

Bloodworms were dispersed throughout the water column and over both the channel and subtidal flats. Nets at all stations and depths captured worms. The average number netted was three and ranged from one to seven. Of the 72 worms from all cruises, nets set in the channel contained 58 worms and those over the subtidal flats held 14. Their numbers decreased vertically: 33 near the surface, 17 at 3 m, 15 at 10 m, and 7 near the bottom.

An exceptionally large catch per unit effort was obtained on 10 December. During the 10 cruises the nets strained approximately 8,000 to 20,000 m^3 of tidal water per cruise. Five of the sets yielded catch rates varying from 0.1 to 0.7 worm/1,000 m^3. A sixth set (10 December) yielded 3.38 worms/1,000 m^3. This catch rate was sufficiently large to permit comparison of synoptic catch rates with location and depth. The four lines of nets in the channel strained 39 worms from 10,194 m^3, yielding a catch rate of 3.8 worms/1,000 m^3. Those nets

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

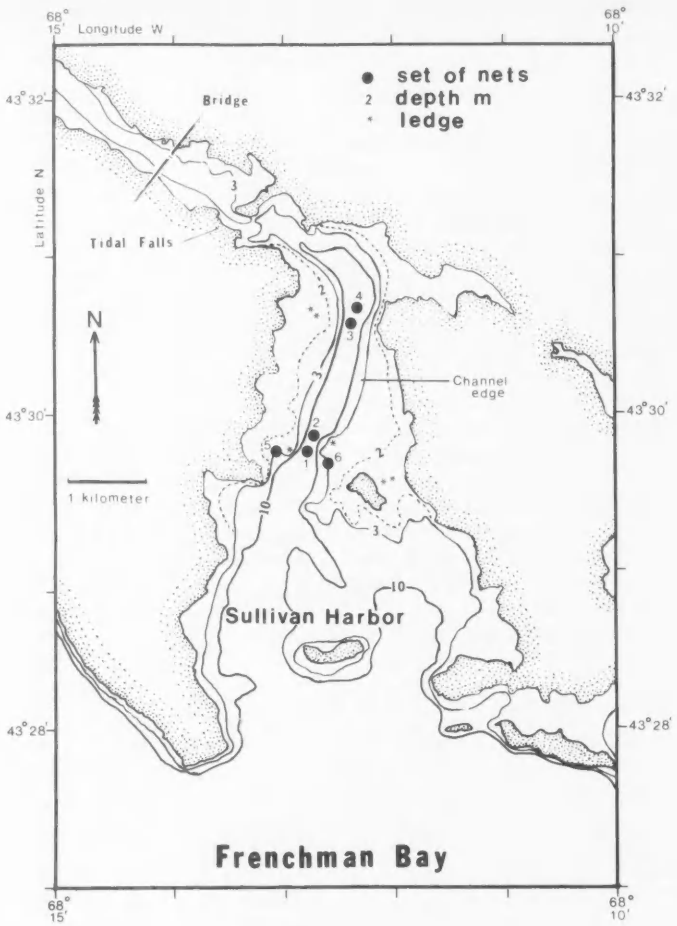

FIGURE 1.—Sampling stations (1-6) for larval Atlantic herring with sets of buoyed and anchored nets in Sullivan Harbor, Maine.

in the flats strained 12 worms from 4,889 m^3, yielding 2.4 worms/1,000 m^3. Shallow nets, above the channel edge and those near the surface of the flats, captured 37 worms by straining 9,614 m^3 for a catch rate of 3.8 worms/1,000 m^3. Deep nets, below the channel edge and those near the bottom of the flats, captured 14 worms by straining 5,469 m^3 for a catch rate of 2.6 worms/1,000 m^3.

The numbers of worms captured in the nets were few when compared with the numbers of smaller tychoplankters, such as amphipods. Each individual weight, however, was relatively large compared with those individuals of more numerous taxa and suggested that a large biomass of bloodworms sometimes enters the water column of the harbor.

Discussion

The mature bloodworms captured during winter in buoyed nets at Sullivan Harbor were not free-swimming spawners. Creaser (1973) sampled a small worm flat at Wiscasset, Maine, from November 1967 to August 1969. During that time, among the many worms dug, only three spawners occurred during winter. Analysis of his collections showed that egg diameters increased somewhat during December and January but ceased growth during the colder months of February and March. Spawning was triggered in June by formation of the epitoke, the growth of eggs to the spawning "range" and a water temperature of at least 13°C. These conditions were not found in the present

study. Also, we did not detect any morphological changes that accompany formation of the epitokes as described by Simpson (1962).

Swimming bloodworms at night have also been reported for two other Maine inshore waters. Dean[3] saw 22 bloodworms during observations made between 24 January and 29 March 1977 on 33 nights. The worms were present during five nights in March and 15 were collected under a night-light in the Damariscotta River, Maine—8 on 11 March and 7 on 12 March. The gametes of the worms were not sexually mature and the presence of the worms near the surface at night was not related to spawning. Dean also reported that buoyed and anchored nets set in Montsweag Bay and the Sheepscot estuary between 1970 and present captured 22 glycerids, some of which were *G. dibranchiata*. In contrast, the senior author of this paper did not capture bloodworms in buoyed and anchored nets set in the Sheepscot estuary over the same time period and in the same vicinity. Possibly, the swimming of bloodworms at night is sporadic.

A recent study of residual currents in Sullivan Harbor suggested that the relatively shallow nets above the edge of the channel (Figure 1) and at the surface over the tidal flats strained a residual seaward flow transporting tychoplankters and the relatively deep nets strained a residual landward flow. Distribution of bloodworms throughout the water column would, therefore, insure their wide dispersal by horizontal tidal currents, and it is unlikely that after a tidal cycle they would regain the location of their original burrows.

We hope to study further the bloodworms of Sullivan Harbor and do not wish to speculate on their origin or fate at this time. Rather, it is our purpose to suggest that researchers investigating bloodworms within their bottom habitat should also examine their possible role as tychoplankters for two reasons: populations of this important commercial species in separate flats may become intermixed, introducing problems in their management; and the reestablishment of worm populations previously destroyed by pollution or other environmental catastrophe might proceed more rapidly in those areas where there is winter transport of mature worms, as well as the "normal" dispersion of late spring larvae.

[3]Dean, D. The swimming of bloodworms (*Glycera* spp.) at night. Unpubl. manuscr.

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SIMULATED FOOD PATCHES AND SURVIVAL OF LARVAL BAY ANCHOVY, *ANCHOA MITCHILLI*, AND SEA BREAM, *ARCHOSARGUS RHOMBOIDALIS*

Survival rates of laboratory-reared marine fish larvae often are directly related to prey concentration. Best survival usually has been reported when prey are available at concentrations >1,000/l (O'Connell and Raymond 1970; Laurence

1974, 1977). Houde (in press) recently demonstrated that survival of three species of marine fish larvae from hatching to metamorphosis was 10% or higher when mean prey concentrations were only 34-130/l. But, he also found enhanced survival when food concentrations were increased. For significant numbers of larvae to survive the transition stage from yolk nutrition to active feeding, some researchers believe that dense patches of prey must occur in the sea (O'Connell and Raymond 1970; Hunter 1972). Such patches might occur at densities of 10 to 1,000 times above the mean prey density. Lasker (1975) has discussed the dense patches of the dinoflagellate *Gymnodinium splendens*, which serves as prey for larval northern anchovy, *Engraulis mordax*, in the California Current and their possible relationship to larval survival. Hunter and Thomas (1974) demonstrated that larval northern anchovies were able to remain in patches of *G. splendens* that were artificially created in laboratory experiments.

In two series of laboratory experiments we have examined the effect of two simulated patches of prey on survival in the bay anchovy, *Anchoa mitchilli*, and the sea bream, *Archosargus rhomboidalis*. Patches were simulated during the first 6 days after hatching, when these larvae are most susceptible to starvation mortality. The purpose of the experiments was to determine if prey at high density that were offered for more than some minimum period would result in survival rates of larvae that approached those obtained at a high, constant prey concentration. This would indicate that the larvae were able to obtain a daily ration suitable for maintenance and growth by increasing their feeding rate during the period of exposure to the patch concentration of prey. At the low prey concentrations usually found in the sea, a relatively great expenditure of energy would be required by larvae to obtain the minimum daily ration for maintenance and growth. Such larvae might weaken or fail to grow and thus be more susceptible to starvation or predation.

Methods

Larvae were hatched from fertilized eggs that were collected in plankton nets from Biscayne Bay, Fla. In each experimental trial 140 sea bream eggs were stocked (2.0/l) and 280 bay anchovy eggs were stocked (4.0/l) in a 76-l glass aquarium. Larvae were reared for 10 days at 26±1°C. Salinities ranged from 30.0 to 32.5‰ for bay anchovy and 33.0 to 33.5‰ for sea bream. Lighting was provided at 2500-2800 lx by 40-W, cool-white fluorescent tubes. A 13 h light-11 h dark schedule was maintained. Tanks were isolated in a black plastic enclosure and all light was extinguished during the dark periods. Sea bream and bay anchovy larvae do not feed in the dark. At the end of experiments, survivors were preserved in 5% Formalin[1] and measured using an ocular micrometer.

Prey were the nauplii and copepodid stages of copepods, approximately 50-100 μm in diameter, that were collected in 53-μm mesh plankton nets. Prey concentrations were determined by counting organisms in 100- to 200-cm^3 aliquots from the rearing tank (Houde 1975, 1977) several times per day during the 13-h feeding period. Background (i.e., nonpatch) prey levels were set at 25-50/l; this concentration was maintained when patch concentrations were not offered from 2-6 days after hatching and continuously from 7-10 days after hatching. The patch concentration was 500 prey/l. Patches were provided for periods ranging from 1.5 to 11 h (Tables 1, 2). Both 0 h, at which no patches were provided, and 13h, at which a constant 500/l prey concentration was maintained, also were included in the series of experiments for each species. The patch schedules were maintained for only the first 5 days of active feeding because larvae that survived that period had greatly increased their searching ability and were less dependent on high prey concentrations for successful feeding.

Patches were created by adding prey to obtain the 500/l concentration. After larvae had fed at the patch concentration for the desired period, prey were reduced to 25-50/l by siphoning them out of the system through a 280-μm mesh screen and replacing the siphoned water with 26°C filtered seawater from a 150-l header tank. Sea bream larvae had no difficulty avoiding the siphon and its screen during water exchanges, but precautions were necessary for bay anchovy larvae. A 280-μm mesh partition was used to "herd" anchovy larvae toward one end of the tank prior to each siphoning procedure. Siphoning procedures and water exchanges also were carried out in the 0-h and 13-h patch period experiments to insure that those larvae were exposed to the same procedural disturbances as larvae in experiments where prey concentration was being varied.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Larvae were exposed to the patch concentration twice during each 13-h feeding period to obtain the total desired time at the patch level. For example, for a 6-h patch exposure, the prey concentration was adjusted to 500/l from 0800 to 1100; it was then quickly reduced to 25-50/l, where it was maintained until 1800, when the prey concentration was readjusted to 500/l for the remaining 3 h of the light cycle.

Results

Anchoa mitchilli

Percent survival ranged from 0.36% at 0-h patch exposure to 22.86% at 13 h (Table 1). The steady increase in survival as patch exposure time was increased was described by an exponential function, $Y = 0.3038\ e^{0.3419X}$, where Y = percent survival and X = hours at 500/l prey concentration (coefficient of determination, $r^2 = 0.98$). For the 500/l patch concentration, there was no minimum time of exposure above which larval anchovy survival increased sharply or equalled the survival obtained when larvae were exposed throughout the day to the 500/l prey concentration.

Surviving bay anchovies at 10 days after hatching differed significantly in mean standard lengths (Table 1) among patch exposure times (analysis of variance, $P<0.001$). Mean lengths at 3-, 6-, and 9-h patch exposure times were significantly greater than those at 11 and 13 h (Student-Newman-Keuls test, $P<0.05$).

TABLE 1.—Survival and standard lengths of *Anchoa mitchilli* larvae at 10 days after hatching based on 280 eggs and variable patch exposure times. A patch is a prey concentration of 500/l. Nonpatch levels were 25-50/l. Patch conditions were presented to larvae on days 2-6 after hatching.

Patch exposure time (h)	Survival		Standard length (mm)	
	Percent	No.	Mean	SD
[1]0.0	0.36	1	6.75	—
3.0	0.70	2	7.79	0.17
6.0	1.79	5	7.50	0.68
9.0	9.29	26	7.18	0.64
11.0	13.93	39	6.41	0.76
[2]13.0	22.86	64	6.58	0.58

[1]Food concentration was held constant at 25-50/l during days 2-6.
[2]Food concentration was held constant at 500/l during days 2-6, then reduced to 25-50/l during days 7-10.

Archosargus rhomboidalis

Survival ranged from 3.57 to 66.43% for sea bream larvae over the range of patch exposure times (Table 2). The relationship between percent survival and patch exposure time was described by a power function, $Y = 25.0739X^{0.2878}$, where Y = percent survival and X = hours at 500/l prey concentration. Although the power function described the relationship reasonably well (coefficient of determination, $r^2 = 0.94$), an asymptotic regression might be better to describe the relationship because sea bream larvae exposed to a 500/l patch density for between 3 and 6 h daily apparently survived as well as when the 500/l prey concentration was offered throughout the day. The power function is retained here because fits to the data by asymptotic regressions gave lower coefficients of determination, due to the relatively high variability in observed survival as patch exposure times increased.

TABLE 2.—Survival and standard lengths of *Archosargus rhomboidalis* larvae at 10 days after hatching, based on 140 eggs and variable patch exposure time. A patch is a prey concentration of 500/l. Nonpatch levels were 25-50/l. Patch conditions were presented to larvae on days 2-6 after hatching.

Patch exposure time (h)	Survival		Standard length (mm)	
	Percent	No.	Mean	SD
[1]0.0	3.57	5	4.21	0.44
1.5	22.00	31	4.04	0.56
3.0	32.14	45	3.77	0.56
6.0	59.29	83	3.87	0.40
9.0	41.43	58	3.31	0.41
11.0	66.43	93	4.18	0.28
[2]13.0	42.00	59	4.21	0.31

[1]Food concentration was held constant at 25-50/l during days 2-6.
[2]Food concentration was held constant at 500/l during days 2-6, then reduced to 25-50/l during days 7-10.

Mean lengths of survivors at 10 days (Table 2) differed significantly among patch exposure times (analysis of variance, $P<0.001$), but there was no clear relationship between the mean lengths that differed significantly (Student-Newman-Keuls test, $P<0.05$) and the time of exposure.

Discussion

There was a marked difference in response of bay anchovy and sea bream larvae to the simulated patch conditions. Sea bream survival improved greatly when larvae were presented with prey at 500/l for more than 3 h/day, the observed survival then equaling that when they were offered a constant 500/l prey concentration. Bay anchovies were less successful in using the patch conditions to improve their survival, although increased survival rates did occur when larvae were exposed for more than 6 h to the patch concentration. Results imply that first feeding bay anchovy may require a high and stable prey density to attain best survival in the sea, but that sea bream

are better adapted to survive under fluctuating food conditions.

Survival observed in these experiments can be compared with that reported previously (Houde in press), when survival was related to prey densities that were held constant from day 2 to day 16. Predicted survivals at constant prey densities of 25-50/l and 500/l were 0.72-3.86% and 29.31%, respectively, for bay anchovy larvae; and 5.94-16.61% and 70.45% for sea bream larvae. Observed survivals at 0-h and 13-h patch exposures (Tables 1, 2), which correspond to the 25-50/l and 500/l constant prey concentrations, were only slightly lower than those reported in the constant prey level experiments (Houde in press). The small differences probably were caused by the siphoning and water exchange procedures which did subject larvae to some stress. The similarity of results in the two reports indicates that the patch simulation procedure was effective in demonstrating the impact of patches on larval survival.

Growth results were inconclusive. Significant differences in mean lengths were observed among patch exposure times for both species (Tables 1, 2). In sea bream there was no clear relationship between mean lengths and patch exposure times, but, unexpectedly, bay anchovy mean lengths were smallest at the longest patch exposure times. Presumably only the hardiest larvae survived when patches were presented for only a short time, and these larvae also may have had a relatively great potential for growth. At the long exposures to patch densities, survival was better, but no improvement in growth was noted, possibly because some larvae with relatively poor growth potential survived, or because of density-dependent effects on growth that have been previously observed (Houde 1975, 1977). Another compensating factor was that patches were only presented on day 2 to day 6 of the experiments, the prey concentrations in all experiments being held constant at 25-50/l from day 7 to day 10.

Only one possible patch regime was used in these experiments. It is possible that other patch densities or exposure schedules might alter results or conclusions. An infinite number of possible patch conditions could be simulated but future experiments should be delayed until the temporal and spatial scales of patchiness of organisms consumed by marine fish larvae are better known. Conditions that were simulated in these experiments do not discount the possible ability of larvae in the sea to maintain themselves within prey patches that retain their integrity for days or weeks. Hunter and Thomas (1974) demonstrated that northern anchovy larvae could maintain themselves within small patches of *Gymnodinium splendens* in laboratory tanks. Lasker (1975) found that feeding northern anchovy larvae were relatively more abundant in the chlorophyll maximum layer of the Los Angeles Bight, where *G. splendens* was abundant, than in surface waters, and he suggested that larvae might be able to maintain themselves in this rich source of food. Bay anchovy larvae in our experiments derived small benefits from the patch regime that we provided, but there may be stable patch conditions in the sea which could greatly increase their potential for survival.

Acknowledgments

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DISCOVERY OF JUVENILE PACIFIC SALMON (COHO) IN A SMALL COASTAL STREAM OF NEW BRUNSWICK

Three juvenile Pacific salmon (Figure 1) were discovered in a small coastal stream in southern New Brunswick (Figure 2) in October 1976 while young Atlantic salmon, *Salmo salar*, were being collected for laboratory experiments. The Pacific salmon were not recognized by the electrofishing team, and their presence among the Atlantic salmon was not realized until the fish were sorted in the laboratory some days or weeks later. Identification as either coho salmon, *Oncorhynchus kisutch*, or chinook salmon, *O. tshawytscha*, was later confirmed by W. B. Scott of Huntsman Marine Laboratory, St. Andrews, N.B. Positive identification to species of these juvenile fish was not possible, but they were almost certainly coho salmon because of recent introductions of this species to the Atlantic coast.

Coho salmon are not native to the Atlantic, and no populations reproducing in natural streams of the Atlantic coast are known. Two aquaculture operations using coho salmon are under way in Maine, and coho salmon smolts have been released in streams in New Hampshire and Massachusetts since 1969 and 1971, respectively (Figure 2, inset). Presumably, the parents were from one or more of these four operations. No adults have been reported from New Brunswick streams.

When the coho calmon were recognized, further trips were made to obtain an estimate of their numbers in the stream, their size, and habitat preference in comparison with Atlantic salmon and brook trout, *Salvelinus fontinalis*, which were also present.

The stream, known locally as Frost Fish Creek, drains into the estuary of the Digdeguash River about 250 m from the Digdeguash Falls. It is a small stream approximately 3 m wide in the lower kilometer where all fishing took place. Its drainage area is approximately 570 ha. Discharge during low summer flow reaches as little as 80 l/s (Symons and Harding 1974). The lowermost 0.25 km is steep with cascades and pools. The stream here is either open to the sky or overhung with alders. Most of the Atlantic salmon yearlings occur in this portion of the stream. Through the next 0.25 km upstream the gradient decreases; occasional riffles are separated by pools and slow-flowing water. Bankside cover consists of coniferous softwoods partially clearcut. Atlantic salmon yearlings and underyearlings occur in the riffles of this section while the pools and quieter water are inhabited by brook trout. Above this section the

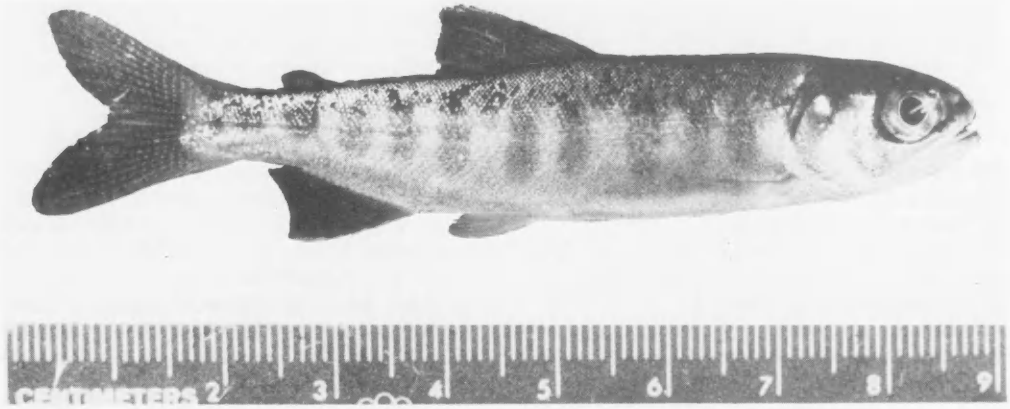

FIGURE 1.—Underyearling coho salmon captured on 28 October 1976 in Frost Fish Creek, N.B.

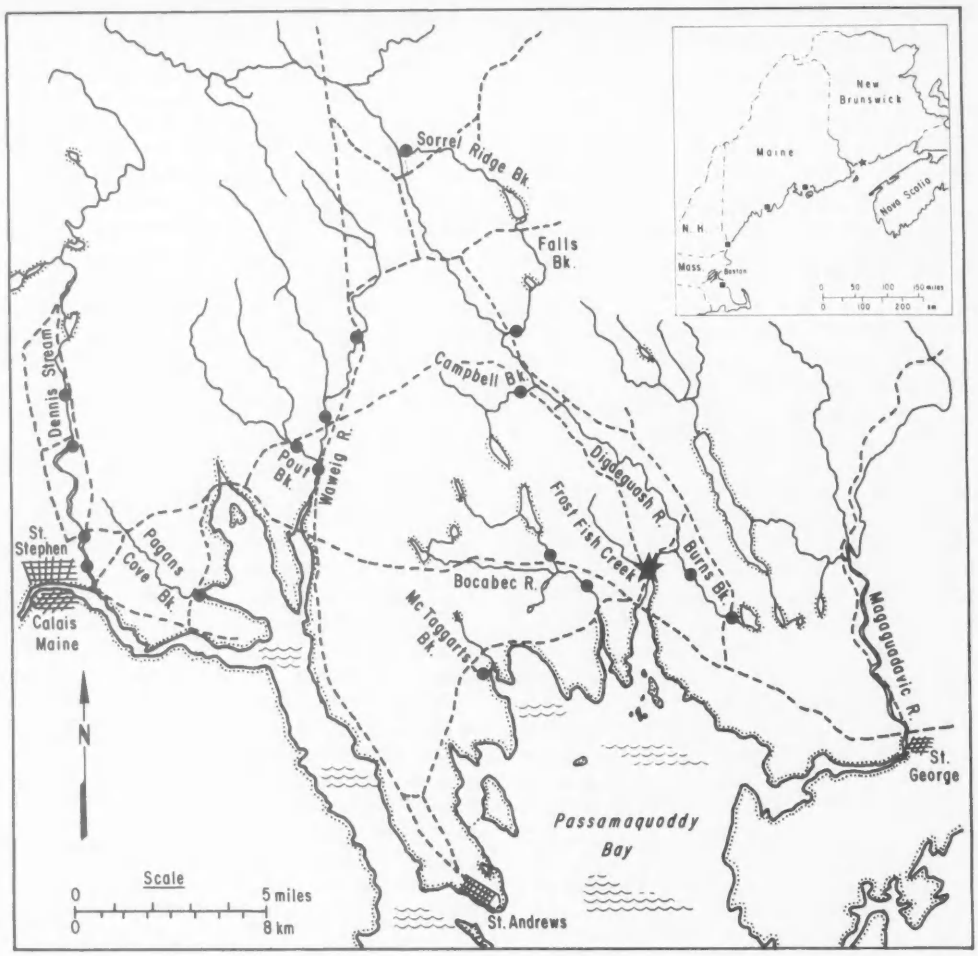

FIGURE 2.—Streams of southern New Brunswick and their access. Dots, sites of spot checks; star, site where coho salmon were captured. Inset, province of New Brunswick, Canada, and northeastern United States showing location of aquaculture operations (Maine) or release sites (N. H. and Mass.) of coho salmon (squares) with respect to location of underyearling coho salmon discovered in New Brunswick (star).

stream gradient becomes lower, the surrounding area is swampy, the stream is choked with alders and inhabited almost exclusively by brook trout. Coho salmon occurred through the middle riffle-pool section and extended in diminishing numbers into the swamp area upstream.

To estimate the numbers of young coho in the creek, two equal-effort electrofishings were performed through the riffle-pool section and approximately 50 m into the swampy section. The lower fast section was fished separately during the first trip (28 October), but since it contained no coho salmon it was omitted on the second 20 days later. Although some coho salmon might have moved downstream in the period between the two fishings, coho salmon were scarce in most upstream areas on both occasions, suggesting there were few above the point where fishing ceased. Twelve coho salmon were caught on the first trip and five on the second. The total population estimated by the depletion method (Seber and Le Cren 1967) was 21. Three coho salmon had been cap-

tured during the collection trip on 9 October, so that the total estimated population of coho salmon in the stream was 24.

During electrofishing, particular note was taken of the kind of habitat in which coho, Atlantic salmon, and brook trout were captured. Coho salmon were found where there was immediate or nearby overhead cover in the form of overhanging banks, tree roots, or fallen trees or brush, and where the water current was slow (<30 cm/s). This kind of habitat was also frequently occupied by brook trout. On at least one occasion, a brook trout and coho salmon were captured together. Atlantic salmon were scarce above the lowermost steep section of the stream. However, in October and November three or four Atlantic salmon were captured in slow water where they had never been seen in summer (Symons and Harding 1974). These observations suggested that summer habitat requirements of coho salmon were more similar to those of brook trout than of Atlantic salmon, although the latter may utilize brook trout-coho salmon habitat in winter.

All captured coho salmon were retained and taken to the laboratory for measuring and weighing. The average fork length of all coho salmon captured was 89 mm, ranging from 75 to 100 mm. There was no statistical difference between average lengths in October (89 mm) and in November (91 mm). Examination of scales revealed that these coho salmon were underyearlings. They were considerably larger than underyearling Atlantic salmon (60-70 mm fork length) and underyearling brook trout (40-60 mm) captured at the same time. The coho salmon were retained for use in laboratory experiments through the winter, and the 10-15 that survived were returned to Frost Fish Creek the following April.

To investigate whether coho salmon might be present elsewhere, spot checks were made in 17 nearby locations (Figure 2) between 28 October and 17 November. Spot checks consisted of 10-35 min of electrofishing with most effort being expended in parts of streams having habitat similar to that in which coho salmon were caught in Frost Fish Creek. No coho salmon were found at any of these sites. Brook trout were caught in all streams, and Atlantic salmon were caught in streams where they were known to occur. Brown trout, *Salmo trutta*, were caught in Frost Fish Creek (2 individuals), Burns Brook (1), and Sorrel Ridge Brook (1), all tributaries to the Digdeguash River. Brown trout were introduced to the Digdeguash as early as 1921 (MacCrimmon and Marshall 1968), and they continue to exist there in small numbers.

In sum, an estimated population of 24 underyearling coho salmon was found in Frost Fish Creek in fall 1976. No coho were discovered in neighboring streams during a cursory search. Although adult coho salmon are known to spawn in small, gravelly coastal streams (Scott and Crossman 1973), spawning may not have occurred in the creek. Atlantic salmon apparently do not spawn there despite the presence of young which are thought to arrive from the main Digdeguash River, having descended the falls into the estuary and then reentering the nearest available freshwater. The young coho salmon may have arrived by the same route. Regardless of the exact location in which coho salmon spawned, should they establish a run in the river system, it would probably be revealed by continued sampling of fish in the creek.

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SUBSAMPLER FOR ESTIMATING THE NUMBER AND LENGTH FREQUENCY OF SMALL, PRESERVED NEKTONIC ORGANISMS[1]

When many samples, containing large numbers of organisms, must be processed it is often necessary to take subsamples and assume that they are representative of the total sample. Frequently subsamples are taken in some arbitrary fashion which is described in such terms as "100 fish were randomly selected." However, it is doubtful whether any selection can be adequately random. Therefore, numerous devices have been designed in attempts to secure more representative subsamples and to increase the speed and efficiency of subsampling.

Most subsamplers have been designed for use with plankton, small benthos, and invertebrate drift samples and are generally unsuitable for larger organisms. However, Lewis and Garriott (1971) modified a Folsom plankton splitter for use on meter net samples containing larval fish up to 19 mm long, and Hightower et al. (1976) described a subsampler specifically designed for use with nektonic organisms.

In the present paper I describe the design, operation, and efficiency of a subsampler originally built for research on estuarine nekton (Herke 1971). The subsampler proved to be useful for estimating the number and length frequencies of small nektonic organisms such as the bay anchovy, *Anchoa mitchilli,* tidewater silverside, *Menidia beryllina,* and brown shrimp, *Penaeus aztecus,* as well as young of larger species such as gulf menhaden, *Brevoortia patronus,* and Atlantic croaker, *Micropogon undulatus.* Although different from most subsamplers, the design is fairly similar to that described by Hightower et al. (1976); it bears some similarities to those described by Hewitt and Burrows (1948) for subsampling live hatchery fish, by Cushing (1961) for plankton, and by Södergren (1974) and Hickley (1975) for benthos.

My sampler differs from that of Hightower et al. (1976) in at least four respects: 1) it has fewer moving parts; 2) fewer water jets are required to achieve through mixing of the sample; 3) a central pillar or cylinder prevents organisms from clumping in the center; and 4) the total sample is subdivided by raising vanes through the mixed sample, rather than allowing the sample to settle into baskets. Also, spin-dry weighing is required, but it takes <1 min to complete the subsampling process (after the organisms are placed in the subsampler), rather than several minutes as required for the subsampler described by Hightower et al. I have made no comparative tests between the two subsampler designs, however; individual circumstances may determine which would be most practical in any given situation.

Subsampler Construction

My subsampler can be constructed of various materials, and the same general design can be used for large and small models. A small Plexiglas[2] version (Figure 1) has an outside diameter of 305 mm, and Herke (1971) also illustrated one with a 580-mm outside diameter that utilized part of a 208-l steel drum for the outer cylinder, a 19-l bucket for the inner cylinder, and plywood for the false floor.

The subsampler in Figure 1 was constructed primarily of Plexiglas about 6 mm thick. Plexiglas joints were bonded with solvent (methylene chloride and trichlorethylene). The major parts and their functions are as follows (numbers refer to the parts labeled in Figure 1):

1. Base.
2. Brass hinge for attaching base to edge of table top.
3. Outer cylinder bonded to base; in addition to solvent, a suitable cement may be required to ensure a watertight seal to the base.
4. Central pillar of Plexiglas tube bonded to base at exact center of circle formed by the outer cylinder (3).
5. Rubber stopper in (4) to prevent material from falling inside the piller.
6. Inner cylinder, which slides smoothly up and down over (4).
7. Locking pin for holding (6) in the raised position. Rubber bands around (6) and over a peg through the shaft of (7) hold the pin in place (these are omitted from the diagram to avoid cluttering).
8. Vane bonded to (6); the outer edge almost touches the outer cylinder. In the raised posi-

[1]Contribution no. 24 of the Louisiana Cooperative Fishery Research Unit: Louisiana State University, Louisiana Wildlife and Fisheries Commission, and U.S. Fish and Wildlife Service cooperating.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

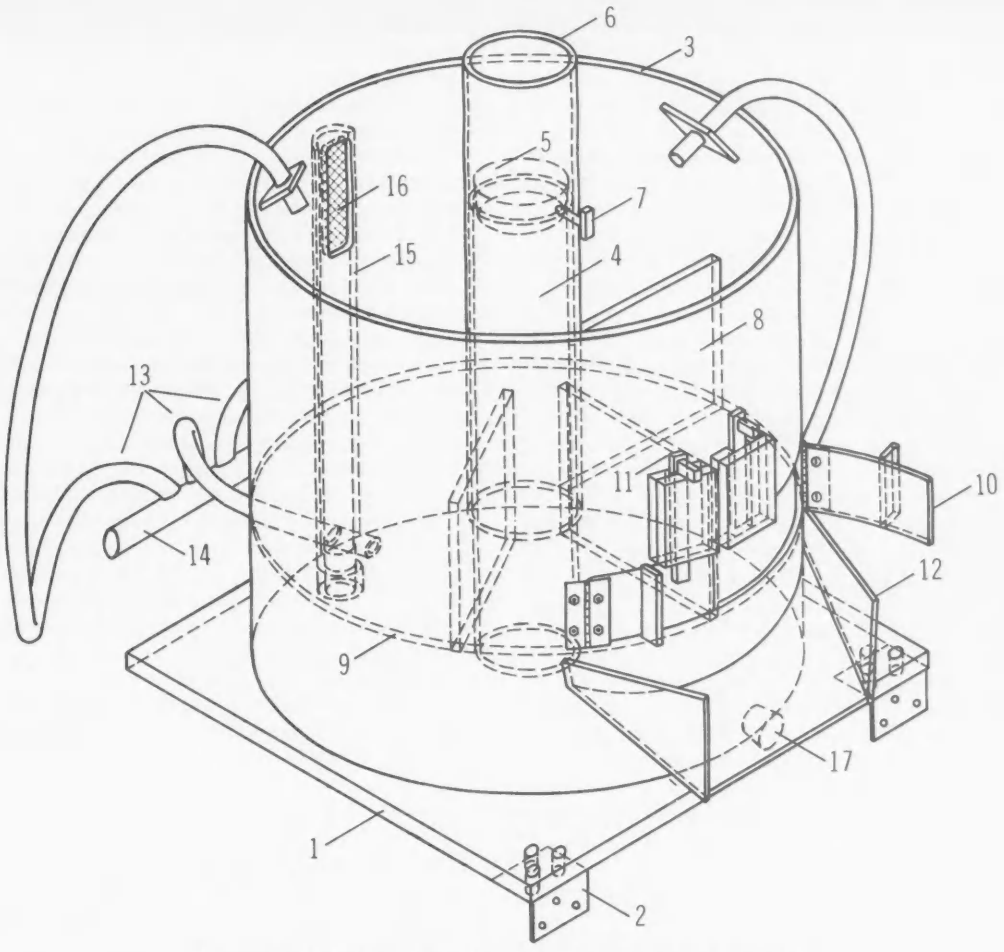

FIGURE 1.—Basic design of the nektonic subsampler; see text for explanation.

tion shown, the three vanes subdivide the sample into portions approximating 0.2, 0.2, and 0.6 of the total.

9. False floor consisting of three sections bonded to the inside of the outer cylinder (3) at a height so that the upper surface is exactly even with the upper edges of the vanes when (6) is lowered to the base. The vanes move up and down through the slits left between the sections of the false floor. Enough space must be left between the inner edges of the false floor and the inner cylinder (6) and its attached vanes to allow the inner cylinder and vanes to move freely up and down. Conversely, the clearance must be small enough to prevent organisms from falling into the space below the false floor. Omitted from the diagram are braces extending from the base to near the inner edges of the two smaller sections of false floor.
10. Hinged door for removing subsampled organisms.
11. Latch holding the other door closed.
12. One side of a spout into which the water and organisms pour when doors are opened; the organisms are collected in a sieve below the spout.
13. Rubber tubes to carry water; the middle one enters the cylinder (3) beneath the false floor (9).

14. Copper tube with outlets for each rubber tube (13). Water to operate the subsampler comes through a large-diameter garden hose and pistol-type hose nozzle (not shown) attached to this tube.
15. Overflow tube attached to the outside of the cylinder (3). The cut edges of a longitudinal section of Plexiglas tubing are bonded to the cylinder from the overflow intake to the bottom of the base (1). Below the base the tube is not sectioned (i.e., left intact) so a drain hose can be attached to it.
16. Aluminum window screen covering overflow intake; bottom of intake opening is level with the top of the vanes (8) when they are raised.
17. Rubber stopper in drain hole below spout.

Also omitted from the diagram are "stops" on the bottom edges of the vanes (which prevent the vanes from pulling through the false floor) and spongy, foam gaskets attached to the doors with rubber cement.

Subsampling Procedure

In subsampling, one pushes the inner cylinder (6) with the attached vanes down until it rests on the base; in this position the tops of the vanes are even with the top of the false floor so that the vanes and floor form a single flat surface. The entire sample is then placed on the false floor. The hose nozzle trigger is squeezed fully open, squirting water rapidly through the rubber tubing. (Normally, the space below the false floor is still filled with water from previous use.) Some of the water rises through the three vane slits in the false floor, thereby inhibiting downward passage of the smaller specimens; most of the water squirts out of the upper tubes, causing the water above the false floor to swirl rapidly. Turbulence thoroughly mixes the sample as both sample and water revolve. When the water almost reaches the bottom of the overflow intake, the inner cylinder (6) and attached vanes are quickly raised as far as possible so that the locking pin (7) slides farther through its hole in (6) and over the top edge of (4); simultaneously, the hose nozzle trigger is released. The sample has now been divided into three parts equal to about 0.2, 0.2, and 0.6 of the whole.

The entire subsampler is next tilted on its hinges (2) in preparation for emptying. If a 0.2 subsample is desired, only one door is opened and the contents of that compartment flow through the spout (12) into a sieve. (To avoid bias, the user should always open the same door first. Occasionally fish balance on top of the vanes; the user can avoid personal bias by always pushing the fish so it falls headfirst.) Opening both doors produces a 0.4 subsample and the remainder of the material in the subsampler constitutes a 0.6 subsample. The 0.6 subsample is removed by first taking out the 0.4 subsample and then lowering the vanes as far as they will go. The 0.6 subsample may then be washed into a sieve below the spout. (When removing any subsample, it is easier to wash the organisms out of the subsampler than to pick or push them out.) A wide variety of subsample ratios can be obtained by sequentially subsampling subsamples (e.g., $0.8 \times 0.2 \times 0.2 = 0.032$).

Small organisms do occasionally fall through the vane slits into the space between the base and the false floor. Such losses are normally insignificant compared with the total number being subsampled, but they are noticeable through the Plexiglas. These organisms may be recovered by washing them out through the drain hole plugged by the rubber stopper (17).

No special leveling of the subsampler is required for proper operation; it may be mounted on any reasonably level surface such as a table top or laboratory bench.

Discussion

The subsampler is useful for estimating both total numbers in a sample and the total length-frequency distribution. If the total sample is not first separated by species, one should at least make a thorough scan of the sample, before subsampling, to remove any unusually large or odd specimens. As stated by Hightower et al. (1976), these can later be added to the total estimate, which is derived by extrapolating the subsample results. However, subsampling can give erratic results for inconspicuous species present in small numbers. Therefore, I think it usually is best to first separate the total sample into individual species, and subsample only the abundant ones. For each of these species, a subsample is first taken, and its weight and that of the remainder are obtained by the spin-dry method described by Herke (1973). (In contrast to plankton, preserved fishes and many crustaceans can be easily and precisely weighed without damage by using the spin-dry method.) All organisms in the subsample are then

counted and the number in the total sample is estimated on the basis of the weights of the subsample and total sample. Since the estimate is based on weight rather than volume, the three vanes need not divide the subsampler into exactly 0.2, 0.2, and 0.6 segments.

If a length-frequency estimate is desired, the subsample can be further subsampled. Since the number in the first subsample is now known, any desired number for the length-frequency subsample can be closely approximated by selecting the proper sequence of subsamples. For instance, suppose the first subsample contains 3,371 anchovies and a length frequency is desired from approximately 100 fish; $3{,}371 \times 0.2 \times 0.4 \times 0.4 = 108$. Therefore, subsamples taken in this sequence should produce the desired number for measuring.

The consistency with which the desired number is obtained may be judged (Table 1) by comparing the "theoretical" and "actual" numbers obtained in 20 successive trials. The two subsamplers used in these trials had a tendency to slightly exceed the desired number; one or both of the smaller compartments in each subsampler probably contained a bit more than 0.2 of the whole. However, the increased subsample size actually improves the probability of obtaining an accurate length-frequency estimate. Also, with use, one soon learns whether the tendency is to obtain more or fewer than the theoretical number and can select the subsampling sequence accordingly.

How well the length-frequency estimates derived from subsampling groups of anchovies and menhaden represented the true length frequencies of the groups was examined by using the Kolmogorov-Smirnov one-sample, two-tailed test, which is a test of goodness of fit. The test involves comparing the observed cumulative frequency distribution from a subsample with the cumulative frequency distribution of the total sample. It is sensitive to any kind of difference between the two distributions—differences in location (central tendency), in dispersion, in skewness, etc. According to Siegel (1956) the Kolmogorov-Smirnov test is definitely more powerful than the chi-square test when samples are small, and may be more powerful in all cases.

The cumulative length-frequency distribution for only one subsample was significantly different ($\alpha = 0.05$) from its corresponding total sample (Table 1). In the other 19 tests, the probability was greater than 0.20 that a divergence of the observed magnitude would occur if the observations were really a random subsample from the total sample (0.20 is the highest probability listed in Siegel's table).

TABLE 1.—Results of 20 tests to determine the correspondence between: 1) the theoretical and actual number of bay anchovies or gulf menhaden in the subsample, and 2) the cumulative length frequency distribution of fish in the subsample and in the corresponding total sample. Subsamples were returned to the total sample after each trial. The cumulative distribution shown in italics (in the same row with the number in the total sample) was the true distribution obtained by measuring every fish in the sample.

Number in total sample	Subsample sequence	Final subsample no.		Standard length in millimeters[1]									
		Theoretical	Actual	15	20	25	30	35	40	45	50	55	60
3,371				*0.539*	*0.772*	*0.821*	*0.861*	*0.914*	*0.957*	*0.984*	*0.995*	*1.000*	
anchovies	(0.2) (0.4) (0.4)	108	133		.481	.797	.835	.880	.947	.970	.977	.992	1.000
			124		.524	.758	.838	.863	.911	.960	.976	1.000	
			134		[2].418	.739	.791	.858	.932	.962	1.000		
			141		.489	.709	.773	.822	.894	.950	.979	.993	1.000
			146		.479	.740	.781	.856	.925	.938	.986	1.000	
1,505				*0.361*	*.553*	*.643*	*.774*	*.846*	*.908*	*.964*	*.991*	*.998*	*.999*
anchovies	(0.2) (0.2)	60	49	.347	.551	.571	.673	.734	.795	.917	.958	.999	
			59	.322	.576	.661	.729	.814	.848	.933	.967	1.001	
			77	.338	.520	.559	.676	.793	.832	.949	.988	1.001	
			70	.357	.528	.628	.728	.799	.885	.956	.985	.999	
			71	.389	.570	.598	.667	.778	.875	.958	1.000		
Same	(0.4) (0.2)	120	128	.328	.586	.672	.766	.836	.914	.992	1.000		
1,505			125	.272	.544	.600	.776	.864	.920	.976	1.000		
anchovies			133	.353	.556	.654	.789	.842	.880	.940	.985	.993	1.001
			134	.306	.507	.589	.768	.843	.903	.970	1.000		
			152	.283	.526	.598	.710	.780	.881	.934	.987	1.000	
1,221								*.020*	*.273*	*.756*	*.980*	*.998*	*1.000*
menhaden	(0.4) (0.2)	98	90					.000	.278	.656	1.000		
			116					.026	.198	.733	1.000		
			115					.017	.252	.765	.991	1.000	
			128					.031	.242	.664	.969	.984	1.000
			113					.027	.345	.796	1.000		

[1]Measured in 5-mm increments; i.e., 15 = 15.0–19.9, 20 = 20.0–24.9, etc.
[2]The probability of a divergence this large in a random subsample from the total sample was between 0.05 and 0.01. The probability for the 19 other subsamples was >0.20.

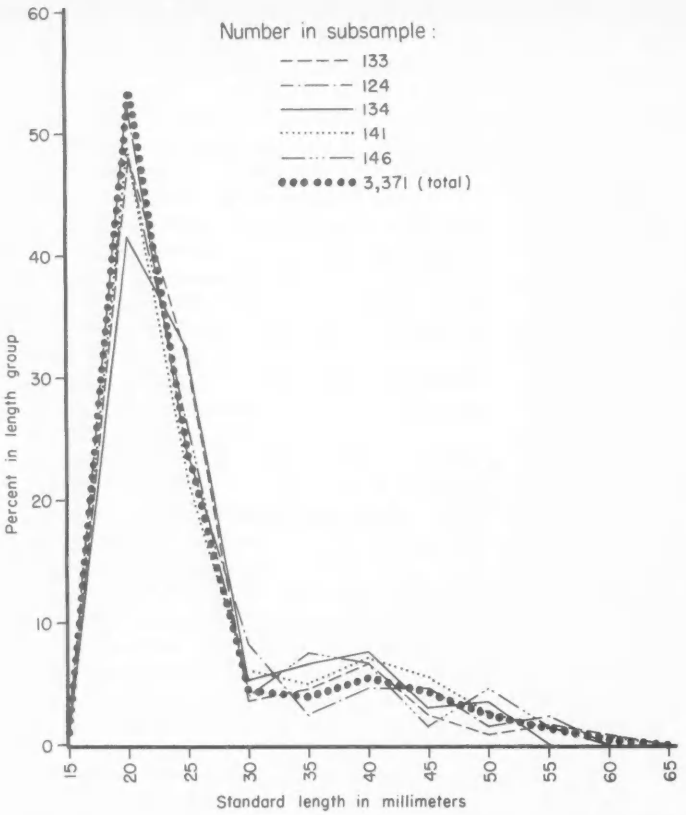

FIGURE 2.—Length-frequency distribution of a total sample of 3,371 bay anchovies, and of each of five subsamples taken from the total. (From Herke 1971.)

It is difficult to visualize, from inspection of the cumulative length-frequency distributions, how well the percentage of fish in each subsample length group represents the percentage in the corresponding length group in the total sample. Therefore, this comparison is shown graphically (Figure 2) for the first five subsamples listed in Table 1.

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Berrien, Peter L., "Eggs and larvae of *Scomber scombrus* and *Scomber japonicus* in continental shelf waters between Massachusetts and Florida," p. 95-115.

1) Page 99, left column, line 9, correct line to read:
or seven pterygiophores in the 2d through 5th (deleting the zero)

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